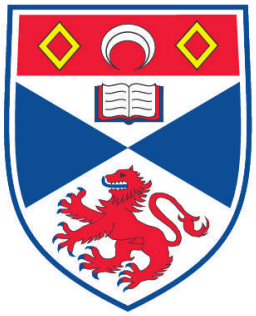
ATTENTION CUES IN APES AND THEIR ROLE IN SOCIAL PLAY BEHAVIOR OF WESTERN LOWLAND GORILLAS (GORILLA GORILLA GORILLA)

Jessica A. Mayhew

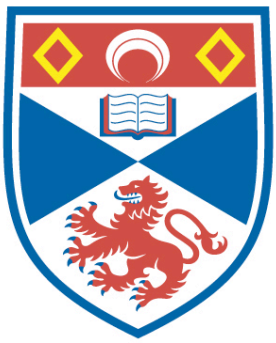
A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews



2013

Attention cues in apes and their role in social play behavior of western lowland gorillas (*gorilla gorilla gorilla*)

Jessica A. Mayhew



University of
St Andrews

This thesis is submitted in partial fulfillment for the degree of PhD
at the
University of St Andrews

December 3, 2012

Declaration

I, Jessica A. Mayhew, hereby certify that this thesis, which is approximately 51,500 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September 2008 and as a candidate for the degree of Psychology in September 2008; the higher study for which this is a record was carried out in the University of St Andrews between 2008 and 2012.

Date 7/4/12 Signature of candidate

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Psychology in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

Date 7/4/12 Signature of supervisor

In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and the abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker, that my thesis will be electronically accessible for personal or research use unless exempt by award of an embargo as requested below, and that the library has the right to migrate my thesis into new electronic forms as required to ensure continued access to the thesis. I have obtained any third-party copyright permissions that may be required in order to allow such access and migration, or have requested the appropriate embargo below.

The following is an agreed request by candidate and supervisor regarding the electronic publication of this thesis:

(i) Access to printed copy and electronic publication of thesis through the University of St Andrews.

Date 7/4/12 Signature of candidate

Date 7/4/12 Signature of supervisor

Acknowledgements

This dissertation would not have been possible without the guidance and support of many people on both sides of the Atlantic. I would like to thank my colleagues at St Andrews, particularly those in the Wolfson lab, for thoughtful discussions and sharing in both the triumphs and difficulties of the PhD process. Many thanks go to Andy Whiten and Klaus Zuberbühler for their helpful comments and critiques on this project during its initial stages. A big thank you also goes to Professor Richard Byrne and Dr. David Leavens for a positive and inspiring viva and the many insightful comments and queries about this work. Thanks to Ken Munro for the development of the "Gape" program, and to the participants in the experimental Bogart studies. Thank you to David Mackey at Plymouth State University for taking the time to answer questions about statistics. Thank you to Kirsten Pullen from the Paignton Zoo and Julie Mansell from the Belfast Zoo for contributing their gorilla groups to the white sclera study.

A tremendous thank you goes to Dr. Juan-Carlos Gómez for his advice, for reading through countless manuscript revisions, and most of all, for his incredible patience throughout this entire process. I am grateful to Dr. Dario Maestripieri for his encouragement and for mentoring me in my time while at The University of Chicago. His dedication to and enthusiasm for research motivated me to pursue this PhD. A big thank you goes to Jason Watters for welcoming me to the Brookfield Zoo and introducing me to each member of their wonderful gorilla group. It was an absolute pleasure to spend my summer there. A thank you also goes to Craig Demitros for taking the time to talk gorilla with me.

My time in Chicago would not have been possible without the generosity of Jen for sharing her living room and refrigerator with me. I am eternally grateful for her friendship and love. Thank you Cass, for teaching me the significance and beauty of friendship, and to Arbi for his continuous excitement about having a monkey scientist for a friend. To Chad, *mi media naranja*, it has been a long journey, and I thank you for always meeting me at the airport.

Thank you Charlie and Lu for being my home away from home and for being the most generous and caring people I've ever had the pleasure to know. Thank you to Debbie for her never-ending support and always kind and loving words, and to my Grandma for her reminders of how proud she is of me. To my parents, who have provided me with the opportunity to pursue academics without question and with the utmost support. There are not enough ways to thank you for always being excited and encouraging of my nerdy babbling. To Bry and Critter, your constant questions about primates and suggestions for new and unconventional avenues of research have always been appreciated. Thank you for dinnertime discussions that are nothing short of brilliant.

And finally, to all of the animals in my life, especially Schaefer and Hails ("Spooky"), who have inspired me to keep looking for a way to get to know them better.

Abstract

Attention cues in apes and their role in social play behavior of western lowland gorillas (*Gorilla gorilla gorilla*)

The research aims of this thesis are to investigate the attention cues available to and used by apes, especially gorillas (*Gorilla gorilla*), to ascertain the direction of conspecific attention during social interactions with a special reference to social play. Minimal research has been conducted on the role of attention cues – eye gaze, head, and body orientation – to regulate natural social interactions, such as social play, in non-human primates. This thesis begins with an investigation of the "cooperative eye hypothesis", which poses that humans have evolved a unique white sclera adaptation for advertising and detecting gaze direction. Chapter 2 reports the existence of a natural white sclera variation in a proportion of gorilla eyes – contradicting the widely held assumption that white sclera is an exclusively human characteristic – and analyzes the presence of white sclera in relation to other morphological changes in the human eye. The study concludes that the morphological elongation of the eye might be a more important and unique change than the white sclera coloration. Chapter 3 experimentally explores the contribution of white sclera in both great ape and human eye gaze to the perception of gaze direction detection by human observers. This chapter concludes that although white sclera contributes to the accuracy and speed of gaze direction detection (an assumption that this thesis has put to experimental test for the first time), this merely adds to the already efficient gaze cues available in the eye areas of the ape face. Chapter 4 investigates the role of eye gaze, head, and body orientations during gorilla social play behavior, and more specifically, introduces a novel analysis of "vigilance periods" (VPs),

in which gorillas may use the interaction between attention cues to gauge the attention and intentions of play partners to successfully navigate play. The final study (Chapter 5) complements Chapter 4 and investigates the role of gorilla postures, behaviors, and movements during changes in attentional cue orientations. This chapter concludes that gorillas often engage in physical rest during VPs but maintain attentional engagement and can assemble and impart socially relevant information based on behaviors, movements, and attention orientations of their partner. Together, these studies suggest that attention orientation is conveyed and assessed by gorillas through a variety of interacting cues to navigate and modify social play interactions.

Figures and Tables

CHAPTER 1:

General Introduction

Chapter 1: General Introduction

1. Primate vision

Vision is one of the fundamental senses that enable an animal to connect with the surrounding environment. As a primary sense for primates, vision contributes greatly to the gathering and processing of environmental information that is crucial for survival. The forward rotation of primate eyes results in overlapping fields of vision and produces a wide binocular field (Martin, 1990). This high orbital convergence corresponds with stereoscopic processes, which combine the individual two-dimensional input received from each retina and reconstruct the input information into a three-dimensional mental representation. The overlapping visual fields increase visual acuity, particularly within environments containing low levels of light (Ankel-Simons & Rasmussen, 2008; Heesy, 2009; Ross & Kirk, 2007). Discrepancies between the visual inputs of each eye provide depth information about the object or environment that is viewed. Both the increase in visual acuity and depth perception abilities are especially beneficial for fine prehensile actions, particularly when considering the arboreal locomotion or fine manual foraging techniques common to many primate species (Heesy, 2009; Ross & Kirk, 2007). Trichromatic color vision is also a common feature of Old World monkeys, apes, and humans, although there is intraspecific variation of color vision in some diurnal New World monkeys and lemurs, i.e., all males and some females are dichromats, but some other females are trichromats. One proposed hypothesis for a color vision adaptation is that it enhances the ability to forage on and manipulate colorful fruits and leaves (Barton, 1998; Bradley & Mundy, 2009; Vorobyev, 2009).

In the primate eye, external visual information follows a complex pathway leading from the retina through the visual processing regions of the brain. The complex neural hardwiring of the visual pathway organizes visual input of the surrounding environment into usable information that allows an individual to successfully interact within their present space. Ongoing neurological research has revealed that specific visual regions in the brain contain populations of cells that exhibit specific sensitivities to the different attributes of a visual stimulus, e.g., shapes, sizes, colors, contrasts, movements, and orientations (Dubuc, 2002; Perrett & Emery, 1994; Perrett *et al*., 1992; Perrett *et al*., 1985).

However, vision is more than a self-serving neural process of three-dimensional mental representations of environmental visual inputs. The process of "seeing" can be highly complex, especially when considering the behavioral aspects of vision that are required to "see" effectively. While the eyes are the organs that connect surrounding environmental stimuli to the brain, the alignment and coordination of the eyes, head, and in some cases body postures and movements, play pivotal roles in the effective viewing of the environment. Not only does seeing require the eyes to maintain on a particular stimulus, but also often involves an according head and body orientation to achieve an optimal visual trajectory. For example: a gorilla play partner that wants to socially reengage approaches its partner from the left side on the fringe of the partner's peripheral vision. The eyes of the partner are capable of peripheral gazing, yet adjusting the head to rotate the eyes toward the approaching partner improves the quality of the visual input. The environmental target – the play partner – becomes the object of visual focus through a

complex sequence of gazing behaviors – the coordinated rotation of the eyes, head, and maybe the body – that can be designated as *visual attention*.

Attention can convey valuable information to both the individual that is attending to a specific target and also to an individual close enough to visually monitor eye gaze. In addition to the input of one's own visual system, primates also receive vital survival information gleaned from the gaze of conspecifics, which informs about the location of potential predators, foraging opportunities, etc. For social primates, the detection of and determining the direction of eyes within the environment can also inform about socially relevant information related to a variety of social interaction possibilities including play, copulation, aggression, and competition. However, to gather any of this environmental information and apply it in a useful manner, specific gaze processing faculties are essential. Therefore, it would be of great adaptive advantage if the brain could not only compile surrounding environmental visual input but also process this information within a social context to facilitate a further perceptual understanding of conspecific gaze. One primary interest of this dissertation is to examine the types of adaptations that social primates, specifically western lowland gorillas (*Gorilla gorilla gorilla*), have acquired to ascertain the presence and direction of conspecific attention.

2. Gaze-following mechanisms

Often, the eyes have been colloquially remarked on as being "windows into the soul"; specifically for humans, the eyes are essential when employing "mind-reading" of other individuals (Baron-Cohen, 1994; Gómez, 1991). Baron-Cohen (1994) established a useful framework for a human neurocognitive system of "mind-reading" that originally

comprised of four essential modules, the Eye Direction Detector (EDD), the Intentionality Detector (ID), the Shared Attention Mechanism (SAM) and the Theory of Mind Mechanism (ToMM), and later emphasized the Emotion Detector (TED) and the Empathizing System (TESS), which drew on the recognition and understanding of the emotional states of others (Baron-Cohen, 2004). Although Baron-Cohen's research focuses primarily on a mind-reading system in humans, his modularity of mind framework is useful to illustrate the complex roles that gaze and other cognitive components play in social cognition.

2.1. Detecting eyes and eye-like stimuli

The detection of the presence of eyes within the environment is indispensable to survival for many species because attending to eyes aimed in your direction could potentially mean the difference between propagating with a mate or being preyed on. One specialized module, the EDD, is proposed to detect the presence of eyes or eye-like stimuli in the environment and determine the direction of gaze (Baron-Cohen, 1994 & 2004). Evidence for this basic mechanism, although not necessarily in the form of a module as proposed by Baron-Cohen, has been presented in several studies that demonstrate animal responsiveness to gaze cues (reviewed in Emery, 2000). Sensitivity to gaze has been established in a number of social vertebrates, including birds (Hampton, 1994; Jaime, 2009), mammals (Call *et al.*, 2003; Myowa-Yamakoshi *et al.*, 2003), reptiles (Burger, 1992), and appears to be present in all primate species tested thus far (reviewed by Rosati & Hare, 2009) including some species of prosimians (Ruiz *et al.*, 2009).

Perrett & Emery (1994), who were pioneers in the study of gaze-following skills in non-human primates, further contributed to Baron-Cohen's system and proposed the incorporation of a Direction of Attention Detector (DAD) that would function to determine the attentional direction of others. Evidence for a DAD in relationship to Baron-Cohen's EDD derives from neurophysiological studies in macaques (*Macaca mulatta* and *Macaca arctoides*) with the following evidence shown in cells examined in the superior temporal sulcus (STS): 95.0% responded when a face was presented but not when other objects were presented; 64.0% of the cells were sensitive to the presence of the eye region; and 95.0% of the cells were maximally responsive to a face oriented in a specific direction, e.g., oriented toward or oriented away and to the right (Perrett *et al*., 1985). Further evidence has also shown that cells that are responsive to head orientation are also responsive to body orientation with an overall preference for congruent orientations (Perrett & Emery, 1994).

Based on these results, the authors proposed that a DAD mechanism would take the direction information from the eyes, head, and body and organize it hierarchically to compute attention direction, i.e., visual input from the eyes ranks over directional input from the head, which in turn ranks over directional input from the body. Unidirectional inhibitory connections code the incoming information so that information from eye gaze would inhibit information from an incongruent head orientation, and head orientation would inhibit information from an incongruent body positioning. This hierarchical scheme would be particularly useful in natural scenes where the receiver would need to judge a partner's attention direction from a distance or in the presence of an obscuring

obstacle that blocks attention information (Langton *et al.*, 2000; Perrett & Emery, 1994). In the instance where eye information is not readily available, head and body orientation cues can be drawn on to determine a partner's direction of attention. This graded organization complements and extends Baron-Cohen's emphasis on the importance of eye gaze direction in higher-order perspective taking (Baron-Cohen, 1994; Langton *et al.*, 2000).

2.2. Additional cognitive mechanisms

The eye detection and direction assessment mechanisms would then be further complemented by other cognitive mechanisms. Perrett and Emery (1994) also proposed the presence of a Mutual Attention Mechanism (MAM), which detects the dyadic relationship of mutual gaze between individuals. The authors suggest that the coupling of MAM (mutual attention) and DAD (directed attention) would then give rise to SAM, which is suggested to code triadic relationships between the observer, a partner, and an object of shared attention and allows an individual to recognize that s/he is attending to the same object as a partner (Baron-Cohen, 1994; Perrett & Emery, 1994).

Hypothetical mechanisms, such as the EDD, DAD, MAM, and SAM, have been suggested to act as crucial precursors to a ToMM, in which such mental state knowledge functions to comprehend, interpret, and predict future actions guiding social interactions (Baron-Cohen, 1994, 2004; Tirassa *et al.*, 2006). Researchers remain interested in higher-order cognitive mechanisms in terms of deciphering what animals know about

themselves and those within their environment[1] (Emery & Clayton, 2001; Emery *et al.*, 2004; Hare *et al.*, 2000, 2001, 2003; Horowitz, 2011; Kaminski *et al.*, 2008; Péron *et al.*, 2008; Premack & Woodruff, 1978; Scerif *et al*., 2004). The ontogeny of the necessary modules/mechanisms for a ToMM in humans would progress in a natural sequence of events as the individual ages (*human infants*: Tirassa *et al.*, 2006) and an EDD-like mechanism and eye gaze appear to be integral components.

3. Gaze-following

The ability to gaze follow has been reported not only for our closest primate relatives but also in more distantly related mammalian and avian species. Gaze-following is formally defined as the ability of individual A to follow the gaze direction of individual B to a position in space (Emery *et al.*, 1997; Itakura, 2004). The distinction in the literature between *spatial gaze-following* abilities and *geometrical gaze-following* abilities also typically denotes a distinction between cognitive capacities. Gaze-following around a visually imposing barrier has only thus far been demonstrated in a few species – namely ones that have been deemed more cognitively advanced, such as corvids and great apes – and accordingly, geometrical gaze-following is considered to be more cognitively demanding (Povinelli & Eddy, 1996; Schloegl *et al*., 2007; Tomasello *et al*., 1999).

Two tentative models have been proposed for how and why gaze-following may occur. The *orienting-response model* proposes that an animal just tends to look reflexively

[1] The exploration of possible precursors of ToM has been primarily primate-centric since Premack & Woodruff's (1978) seminal paper "Does the chimpanzee have a theory of mind?" Recently however, experimental cooperative ToM paradigms have extended outside the primate lineage with advancements in both canid and corvid social cognition.

where a conspecific is looking, orienting their own gaze with that of another to detect occurrences within the environment (Povinelli & Eddy, 1996). The second model, the *perspective-taking model*, proposes that the gaze follower understands that a conspecific looks in a particular direction because it is seeing something different and interesting from what the follower sees (Bräuer *et al.*, 2005; Rosati & Hare, 2009). These models represent two cognitively distinct ideas: one suggests an unsophisticated automated response, whereas the other implies higher order cognitive abilities of perspective taking. Contributing to the perspective taking motif is the concept of "Brentanian intentionality", which reasons that the evolutionarily advantageous adaptation of gaze-following in primates is not a computation of unobservable mental representations of attention "…but rather the perception of a configural relationship between agent and object" (for an in-depth discussion of Brentanian intentionality and ToM see Gómez, 2008).

However, in regard to ToM, the task of determining whether primates compute abstract mental states or rely on more basic behavioral reading of conspecifics is beyond the scope of this dissertation. This dissertation will focus on the types of attentional cues that are available to and used by apes, particularly gorillas (*Gorilla gorilla*), to determine the direction of conspecific attention during social interactions with a specific focus on social play. The above cognitive models are instead, simply illustrative of how experimental paradigms have been shaped to evaluate the differences in gaze-following abilities in a number of socially living vertebrates, e.g., incorporating visual barriers in the experimental framework to evaluate "perspective taking".

3.1. Birds and reptiles

Despite the evident lack of research that avian and reptile gaze-following has received, those studies that have been conducted have contributed interesting and significant insights into bird social cognition. Both Northern bald ibises (*Geronticus eremita*) and Greylag geese goslings (*Anser anser*) can readily follow the gaze of a conspecific into distant space, which suggests that this ability is present in both altricial and precocial avian species (Kehmeier *et al.*, 2011; Loretto *et al.*, 2010)[2]. However, when presented with a visual barrier task, Northern bald ibises fail to geometrically gaze follow (this was not tested in the Greylags). The ibises visually co-oriented with their conspecific model at the barrier but did not physically reorient themselves to follow the model's line of sight, thus suggesting that they did not take into consideration that a barrier impairs perception (Loretto *et al.*, 2010). Ravens (*Corvus corax*), however, are quite adept at both following the gaze of a human experimenter spatially and behind a visual barrier (Bugnyar *et al.*, 2004; Schloegl *et al.*, 2007). To geometrically gaze follow, ravens physically reposition their bodies by either walking around or flying to the top of the barrier to see. It therefore appears that some bird species can take conspecific perspectives into account, which is exceptionally demonstrated in the strategies of caching birds such as ravens (*Corvus corax*, Bugnyar & Heinrich, 2005) and scrub jays (*Aphelocoma coerulescens*, Emery & Clayton, 2001).

Spatial gaze-following in Testudines using conspecific gaze has been shown in the first

[2] The time frame that spatial gaze following develops – within ~10 days of hatching for geese – reflects the specific growth and developmental pattern of a precocial species. The development of spatial gaze following could potentially serve as a predator detection strategy and would therefore be more likely to appear earlier in precocial species (Kehmeier *et al.*, 2011). This theory is additionally supported by the emergence of this ability in ravens at the time of fledging (Bugnyar *et al.*, 2004).

study of its kind for the red-footed tortoise (*Geochelone carbonaria*, Wilkinson *et al.*, 2010). Additional studies are necessary before any generalities can be drawn about gaze-following in birds and other reptiles, although the results initially suggest that a spatial gaze-following ability may be present across these species in a more general manner than previously proposed. Such positive results for the Sauropsida group, in combination with the emerging documentation of gaze-following in mammals, suggests the presence of a co-orienting response in a basal amniote.

3.2. Mammals

Mammalian species are particularly advantageous subjects for evaluating gaze-following abilities because of their high sociality. Much of the current research has focused efforts on the primate lineage, although some studies have expanded into other taxa. Domesticated species have been favorable for experimental research because of their easy accessibility and close coexistence with humans. Domestic goats (*Capra hircus*) have been shown to use conspecific gaze to locate objects above and behind them (Kaminski *et al.*, 2010). More advanced experimental paradigms have shown that domestic horses (*Equus caballus*) use a wide range of attention cues, from eye gaze to pointing, to distinguish between an attentive and inattentive human experimenter (Maros *et al.*, 2008; Proops & McComb, 2010). A special interest has been taken in canid cognition, and the past decade of research has provided evidence of multiple adaptations in many realms of cognitive behavior for a social life alongside humans (reviewed in Miklósi *et al.*, 2004). Domestic dogs (*Canis familiaris*) are attentive to the attentional states of others and can learn, comprehend, and use human eye gaze especially when the gaze direction informs about an object of interest within the environment (Bräuer *et al.*,

2004; Call *et al.*, 2003; Gácsi *et al.*, 2004; Hare & Tomasello, 1999; Hare *et al.*, 2002; Kaminski *et al.*, 2012; Miklósi *et al.*, 1998). Studies on socialized wolves (*Canis lupus*) have shown evidence of spatial gaze-following of human gaze from 14 weeks onward and geometrical gaze-following of a dog demonstrator at six months (Range *et al.*, 2011). Further studies with highly trainable cetaceans and pinnipeds have observed that human gaze can be used by dolphins (*Tursiops truncatus*) to identify specific targets (Pack & Herman, 2006; Tschudin *et al.*, 2001; Xitco *et al.*, 2004), but Gray seals (*Halichoerus grypus*) respond more accurately to human gesturing and gross attentional cues than to eye gaze alone (Shapiro *et al.*, 2003).

3.3. Primates

Comparative evidence from experimental gaze paradigms using both human and conspecific demonstrators has shown that many primates tend to use gaze information in some capacity. At a rudimentary level, primates can use the gaze of another for processes such as co-orientation and spatial gaze-following. Studies have demonstrated this in the great apes (*Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*: Bräuer *et al.*, 2005; *Pan troglodytes*: Bräuer *et al.*, 2005; Okamoto *et al.*, 2002; Myowa-Yamakoshi *et al.*, 2003; Tomasello *et al.*, 1998), the lesser apes (*Hylobates pileatus*: Horton & Caldwell, 2006), macaques (*Macaca mulatta*: Emery *et al.*, 1997; Tomasello *et al.*, 1998; *M. arctoides*, *M. nemestrina*: Tomasello *et al.*, 1998; *M. fascicularis*: Goossens *et al.*, 2008), sooty mangabeys (*Cercocebus atys torquatus*: Tomasello *et al.*, 1998), common marmosets (*Callithrix jacchus*: Burkart & Heschl, 2006), spider monkeys (*Ateles geoffroyi*: Amici *et al.*, 2009), capuchins (*Cebus apella*: Amici *et al.*, 2009), ring-tailed lemurs (*Lemur catta*: Shepherd & Platt, 2008), and brown and black lemurs (*Eulemur*

fulvus, *Eulemur macaco*: Ruiz *et al.*, 2009). Humans also readily use eye gaze as a cue to the direction of attention in others, and this ability emerges as early as the 1-year mark (Akhtar & Gernsbacher, 2008). Newborn infants within the first 5 days of life show preference for faces with direct rather than averted gaze (Farroni *et al.*, 2002), and 4-month-old infants better recognize faces that are accompanied with direct gaze (Rigato *et al.*, 2010).

Great apes are also capable of geometrical gaze-following (Bräuer *et al.*, 2005; Povinelli & Eddy, 1996; Tomasello *et al.*, 1999) with some additional evidence in marmosets (Burkart & Heschl, 2006), capuchins, and spider monkeys (Amici *et al.*, 2009). Whether this is a reflection of more sophisticated cognitive abilities, such as perspective taking or ToM, remains a heavily debated topic. Great apes have shown particular sensitivity to available eye information (Hirata, 2010; Kano & Tomonaga, 2009; Myowa-Yamakoshi, 2003), yet their ability to make use of this information is not always positively reflected in the experimental tasks required of them (Hare *et al.*, 2000; Vick *et al.*, 2001). In particular, the object-choice paradigm appears to produce the most inconsistent results, which may actually be a comment on methodological construction and call for species-specific ecological and socially relevant tasks, rather than a lack of performance on part of the ape participants (Lyn, 2010; Mulcahy & Hedge, 2012).

4. Attentional great apes

It has been suggested that *gaze-following* and *attention* are two different socio-cognitive skills and that joint attention requires extra mental processing of an end "object C" in

addition to the followed direction of gaze (Bard & Leavens, 2009; Emery *et al.*, 1997; Itakura, 2004), e.g., gorilla A follows the gaze direction of gorilla B to a hay pile (object C) in the corner of the enclosure. Aligning one's gaze jointly with another individual, including a final point of interest, can be informational not only about directionality but also offers further information regarding a point of interest in the environment. The literature also often times interchanges the terms *joint attention* and *shared attention*, which disregards that some researchers have made and emphasize a subtle distinction between the two (Emery *et al.*, 1997; Itakura, 2004). Shared attention is a combination of both mutual and joint attention in which both the object and one another become the focus of attention. For example, gorilla A knows that gorilla B is looking at the hay pile in the corner, object C, and gorilla B knows that gorilla A is also looking at the hay pile in the corner, object C. This type of attention is therefore slightly more complex and both individuals A and B are required to have knowledge of the opposite partner's attention, or a method for checking that a partner is looking at what they are looking at. In light of the above-mentioned gaze mechanisms that are required to engage in such attentional feats, joint attention would only require the activation of the EDD or DAD, but shared attention would require the activation of an EDD or DAD and MAM mechanism (Baron-Cohen, 1994; Perrett & Emery, 1994).

Beyond the theoretical discussion concerning the underlying cognitive mechanisms, it remains that behaviorally, great apes show an appreciation for the difference between attentive and inattentive conspecifics. Apes appear to realize that gesturing to an inattentive conspecific is ineffective, and therefore, gaining the attention of an individual

is beneficial before continuing any further interaction. Chimpanzees have been observed to persistently use a variety of non-verbal communicative techniques to request specific food items from heterospecifics (Leavens *et al*., 2005), to change their communicative modality depending on the attentional direction of their partner (Liebal *et al*., 2004), and to reposition themselves within a recipient's attentional field and use visual gesturing, rather than actively manipulate a recipient's attentional state (Liebal *et al*., 2009). Similar studies on other great ape species have observed that visual gesturing and facial expressions diminish in frequency if the receiver is not facing them, which again demonstrates sensitivity across the great apes to the attentional state of others (chimpanzees, bonobos, gorillas, and orangutans: Liebal *et al.*, 2004; orangutans: Liebal *et al.*, 2006; gorillas: Pika *et al.*, 2003; gorillas and orangutans: Poss *et al.*, 2006). Although many have concluded that head and body orientations are the cues most likely used, whether the primary cue of attention is eye gaze, head orientation, body orientation, or some combination of the three remains a debatable topic amongst primate researchers.

An initial study observed that chimpanzees were more sensitive to the orientation of the body rather than the orientation of either the eyes or the face. The study observed that an experimenter with her body oriented toward the chimpanzee and her head oriented away received more gesturing than an experimenter displaying the reverse orientations (Povinelli & Eddy, 1996). In a more recent variation of this study, an open/closed eye condition replaced the directed/averted head orientation condition. Again, an attending experimenter received more gesturing than a non-attending experimenter, but this time the apes (chimpanzees, bonobos, and orangutans) showed increased sensitivity to both

the body and head orientation of the experimenter but not to open/closed eyes (Kaminski *et al.*, 2004). One possible explanation for this result is that the body and face carry two different types of social information; as this was a begging task, a body orientation toward the subject may have indicated the experimenter's ability to offer a reward, whereas a face orientation toward the subject may have indicated the potential for communication. To eliminate the "begging" aspect, a further modification of this study offered a food reward in all body orientations. The results showed significance for face orientation as the principal cue of attention, and all great apes tested were observed to accurately judge attentional states based on this cue (Tempelmann *et al.*, 2011)[3].

Despite these results, eye gaze should not be overlooked as a valid informational cue. An in-depth study on the surface eye movements of chimpanzees showed that a variety of movements are exercised (scan, glance, and fixate) in a range of social situations (resting, feeding, and grooming) and in particular, chimpanzees used scanning more frequently during feeding and resting, and a fixated gaze while grooming (Bethell *et al.*, 2007). Importantly, the glances were incongruent with head orientation 70-100% of the time, which suggests that using only head orientation as a cue to attention direction would lead to an incorrect evaluation the majority of the time[4]. Semi-wild and captive Bornean orangutans (*Pongo pygmaeus*) have also been shown to exhibit specific gaze patterns when gazing at conspecifics (Kaplan & Rogers, 2000). The orangutans of this particular

[3] The results of these three studies indicate that careful consideration should be paid to procedural methodologies and experimental set-ups. These studies investigate some of the same fundamental research questions using similar paradigms but ultimately arrive at three contrasting conclusions.

[4] Bethell *et al.* (2007) reports a surprising incongruence between eye and head orientations in 12-21% of gaze fixations, 42-49% of enclosure scans and 70-100% of glances.

study preferred to look at conspecifics using sideways glances with the head angled and oriented away from the recipient. Both studies are a suggestion that the eyes are salient signals for at least chimpanzees and orangutans and should therefore be evaluated independently of the head, thus emphasizing the difference between "eye gaze" and "gaze". Considering the above-mentioned conflicting attentional cue evidence, this thesis accounts for the distinction between eye gaze and head orientation and examines the attention cues available to great apes during social interactions.

5. Play behavior

Learning, understanding, and exploiting particular attentional cues has important implications in all aspects of ape social life. Play behavior may be one such social interaction that provides gorillas with a privileged arena for learning and experiencing attentional cues. This complex dyadic interaction engages gorillas physically, mentally, and socially, and it may ultimately contribute to their socio-cognitive development through repeated interactions with a variety of partners.

5.1. Defining play

Play behavior mixes elements of cooperation, communication, and reciprocity in the actions of all involved participants. During social play between two partners, there is an incorporation of behaviors from outside contexts that introduce elements similar to those during copulation, agonistic encounters, and predation tactics. For example, biting and grappling are prevalent play behaviors but are also observed during aggression, and mounting is observed during copulation but is often a play technique to achieve proximity to a partner. Although decades of research have occurred, the wide

incorporation of outside behaviors in play has caused difficulty for play researchers to agree on a unifying definition. This ambiguity in play-specific behaviors has presently led to play being a phenomenon that is often better described than actually explained (Bekoff, 1972). Some authors have focused on a functional definition, stating that play "functions to develop, practice, or maintain physical or cognitive abilities and social relationships, including both tactics and strategies, by varying, repeating, and/or recombining already functional subsequences of behavior outside their primary context" (Fagen, 1981). Other researchers have taken a slightly different approach and characterized play by focusing on what occurs during play rather than what play is. Therefore, play becomes "all motor activity performed postnatally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and altered temporal sequencing" (Bekoff, 1997). The failure to develop a universally accepted definition has led researchers to use play as an umbrella term for a wide variety of juvenile behaviors (Martin & Caro, 1985), which can ultimately be misleading.

More recently, specific criteria outlining the identification of playful behavior have been developed in attempt to achieve a balanced play rubric that is not too loose so that all behaviors are incorporated but not too rigid so that all relevant behaviors are excluded (Burghardt, 2005). Characteristically, play behaviors maintain certain properties of exaggeration, repetition, and a structural and temporal reordering of motor pattern sequences that differ from any analogous "serious" contexts (Bekoff, 1997; Burghardt, 2005; Fagen, 1981; Martin & Caro, 1985). These characteristics, in addition to the

criteria of spontaneity, endogenous derivation (autotelic behaviors), behaviors that are not fully functional, repetition but not stereotypical performance, and performance while in a relaxed field (Burghardt, 2005), make playful behavior easily distinguishable from behaviors in serious contextual use.

Despite some uncertainties in definitions and criteria, play is a consistent behavior observed across a variety of animal species, although its structure and dynamics can vary widely in frequency and complexity that is dependent on the species observed, the environmental context, and any social restrictions (Pellis & Iwaniuk, 2000). The widespread presence of play suggests a multi-adaptive capacity and vital role in development, particularly within the socio-cognitive realm (Palagi *et al.*, 2007). Play is also by no means a unique phenomenon restricted to large mammalian taxa and has been documented across most, if not all, mammalian species (*reviews*: Bekoff & Byers, 1998; Burghardt, 2005; Fagen, 1981, 1984; Martin & Caro, 1985), birds (Ortega & Bekoff, 1987), and non-avian reptile species such as turtles (Burghardt, 1998).

5.2. Solitary and social play

Play is classically divided into the two broad categories of *solitary* and *social* depending on whether it is performed alone or with a partner(s). Many of the movements and behaviors of solitary play are also used during social play and vice versa. Solitary play is often a blend of various locomotory movements, e.g., running, jumping, somersaulting, leaping, etc. Individuals engaged in solitary play may also incorporate objects from their environment and use various directed behaviors, such as pulling, shaking, smashing, etc., as a means of interacting with them. Solitary play may also include “exploration” or a

nonsocial investigation of the surrounding environment. Exploratory behavior is a "…curious behavior, a cautious investigation of novel stimuli; [that] affords access to environmental information that was not previously available" (Berlyne, 1960). This type of environmental investigation includes *specific exploration* – the extraction of information or learning about whether an object within the environment is prey, predator, nesting material, etc. – and *diversive exploration*, which is devoted to discovering what can be done with an object, e.g., object play (Burghardt, 2005). Solitary play is typically the first to emerge ontogenetically in primate infants and typically takes on the form of assessing and investigating environmental substrates (Baldwin & Baldwin, 1974; Fagen, 1981).

Social play is the more recognizable play model and typically emerges later in development (Burghardt, 2005; Fagen, 1981). This type of play is performed with another individual, most commonly in dyads but triads, etc. also occur. Social play requires a decrease in distance between the partners and lacks any characteristics of agonistic or dominant/subordinate behaviors, although it may utilize behaviors similar to those observed in more serious contexts such as aggression or predation, e.g., biting or wrestling (Bekoff, 1972; Pellis, 1997; Pellis & Pellis, 1996, 1997). Partners involved in this type of play temporarily relinquish any dominant/subordinate relationships and reciprocity and turn-taking between the partners become key to maintaining the interaction. Most commonly, social play between partners involves variable physical contact and fluctuates in its degree of intensity. It blends locomotory movements, including running, leaping and tumbling, with contact behaviors, such as grappling,

slapping and biting, in myriad combinations that vary in duration (Burghardt, 2005; Fagen, 1981). The play interactions analyzed within this thesis focus solely on social play interactions.

5.3. Play functions and hypotheses

Play can have multiple ascribed functions with the suggested principal function differing from species to species (Martin & Caro, 1985). Researchers have long debated the possibilities of an all-encompassing function of such a seemingly purposeless behavior, and long lists have been developed in effort to establish all of the potential benefits arising from this behavior (functional review in Baldwin & Baldwin, 1977; general play review in Fagen, 1981). Proposed functions have been broadly categorized into three main classes: play as motor training, play as socialization, and play as cognitive or sensorimotor training (Martin & Caro, 1985). In turn, these three classes have shaped the series of hypotheses that have given play behavior research a more empirical course.

5.3.1. *Physical training*

The "physical training" and "motor training" hypotheses have been suggested to address the physical aspects of play. Both hypotheses theorize that play behavior functions to increase and maintain physical fitness or motor performance. Through engagement in repeated physical motions during social locomotory play, the partners involved increase the fitness of their physiological systems (Byers & Walker, 1995; Fagen, 1981; Smith, 1982). This includes the strengthening of cardiovascular, muscular, and respiratory systems vital for daily biological functioning. Similarly, the "exercise hypothesis" proposes that play increases the Darwinian fitness of the individual through enhanced

physical fitness, and it is through the strengthening of the physiological whole that fecundity and survival are concurrently improved (Martin & Caro, 1985). Support for a physically based function of play has been empirically demonstrated in five arboreal ceboid monkeys (*Alouatta palliata*, *Ateles geoffroyi*, *Cacajao calvus*, *Cebus capucinus*, and *Saimiri boliviensis*). The use of suspensory postures over non-suspensory postures during arboreal play was observed to increase the flexibility of the joints and thus promoted an enhanced maneuverability on unstable substrates (Fontaine, 1994). Such physical flexibility would allow for more skillful navigation through the environment and in particular, the ability to navigate more efficiently through unpredictable environments.

5.3.2. *Social skills*

In addition to a physical acclimation to exercise, play also establishes important social relationships between an animal and its peers. The "social skills hypothesis" states that play is not vital for the accrual of adult social skills per se, but rather that play enriches the behavioral repertoire of the animal and therefore refines its social skills while also increasing behavioral flexibility (Baldwin & Baldwin, 1974; Brown, 1988; Fagen, 1984). This behavioral flexibility equips an animal with a coping strategy for novel environments, interactions, and partners. The social skills hypothesis predicts that play will occur more frequently with an evenly matched partner and especially with a peer akin to those that are likely to be encountered in adulthood. This naturally varies between species according to adult social structures.

The majority of play behavior in the great apes is dyadic social play displaying intense locomotive sequences and rough-and-tumble behaviors. Social play among captive

western lowland gorillas (*Gorilla gorilla gorilla*) depends on specific social factors such as the age of the gorilla and age and sex of the partner (Brown, 1988). Younger gorillas have been shown to play more frequently with peers of a similar age, and the general frequency of play typically declines as gorillas mature (Brown, 1988). Partner preference has also been shown based on sex, and male-male and male-female play dyads typically occur more frequently than female-female dyads (Brown, 1988; Palagi *et al.*, 2007). These play dyad structures are reasonable observations when considered from a gorilla social structure standpoint. Both male and female gorillas emigrate from their natal group, and while females form strong social bonds with the adult males of their new group, they do not tend to form strong social bonds with the other adult females (Harcourt, 1979; Watts, 1996). As adults, the male-male bond in gorillas is central, which differs from other primate species that have a strong matrilineal influence. Male gorillas may also spend part of their life living in all male bachelor groups; therefore, male-male and male-female playing would be more frequently observed than female-female dyads. These results are consistent with other studies that examine sex differences in play among gorillas (Maestripieri & Ross, 2004; Palagi *et al.*, 2007) and remain consistent with the predictions of the social skills hypothesis.

5.3.3. *Cognitive skills*

5.3.3.1. *Play signals*

Play may also be an important arena for learning the ability to detect and react to the intentions of other individuals through the recognition of social cues that correlate with the initiation, progression, and outcome of the interaction (Bekoff, 1972, 1997; Palagi *et al.*, 2007). Play-specific signals allow an individual to distinguish between playful and

aggressive interactions. These cues can inform a recipient about the actor's mood and interaction intentions and can also subsequently influence the recipient's own mood and intentions (Pellis & Pellis, 1996, 1997). The well-noted examples of play-specific signals are the "play bow" in canids (Bekoff, 1995 & 1997) and "play face" in primates[5] (Aureli & Whiten, 2003; Chevalier-Skolnikoff, 1977; Fagen, 1981; Flack *et al.*, 2004; Parr, 2005; Pellis & Pellis, 1997; Preuschoft, 2000; Smith, 1978, 1984; Van Hooff, 1973; Waller & Cherry, 2012; Waller & Dunbar, 2005). It is commonly accepted in the literature that when such play signals are used, they aid in the initiation of play ("I want to play"), establish and maintain a playful context ("I still want to play"), and punctuate the play interaction at variable temporal intervals. These specific behaviors reaffirm that in general, all of the behaviors that are performed are playful although they can possibly be conceived as aggressive within an alternate context (Bekoff, 1995). This is especially important for more dangerous behaviors, such as biting, grappling, slapping, or actions directed toward sensitive areas, namely the face, head, and genitals.

An analysis of the frequency of play in captive gorillas (*Gorilla gorilla gorilla*) and bonobos (*Pan paniscus*) observed differences between the play frequencies of two differing social conditions: food distribution and space availability (Palagi *et al.*, 2006 & 2007). Primarily, the mean frequency of play was highest immediately before food distribution and then dropped once food had been introduced to the enclosure. Secondly, the incidence of play face signaling during play fighting increased when partners were in

[5] Pellis & Pellis (2011) remark that not all primate species use the "play face" to initiate play, citing one species, the black-handed spider monkey (*Ateles geoffroyi*), that uses head-shaking instead. Pellis & Pellis (1997) and Pellis *et al*. (2011) further comment that the primate play face, although accepted as an unambiguous marker of play within the research, is actually a poor, true play signal, because the open mouth is a precursor to biting behavior, which is common in primate play fighting.

a smaller indoor enclosure than one that provided more room. Both studies illustrate how play can be used flexibly to address two different potentially tense social scenarios.

The higher incidence of play before food distribution may possibly have been a mechanism to ease social excitement or stress associated with feeding times. The higher incidence of play signaling may have been flexibly employed to appease conspecifics during play fighting while in more confined quarters (Palagi *et al.*, 2006 & 2007). The risk of play fighting escalating to aggression increases as the enclosure size decreases and the ability to escape unscathed diminishes. Similar play signaling studies of social play in canids show that the play bow frequency increases as the intensity of play increases (Bekoff, 1995). Therefore, increased play-specific signaling may work to keep the interaction benign even if the social conditions change. Another example of play-specific signaling may be the high frequencies of chest-pounding in gorillas that occurs in conjunction with social play (Brown, 1988; Maestripieri & Ross, 2004). The chest-pound may act as a behavior to solicit play from a partner while simultaneously informing the partner that the behaviors that follow will be playful. However, chest-pounding is also used within aggressive displays, so more general contextual signals may accompany this ambiguous behavior to signal the difference between a playful and aggressive display.

5.3.3.2. *General contextual signals*

In addition to play-specific signals, other more general context signals may also inform partners about the more immediate actions or intentions, such as approaches, retreats, and attentional states. This social information may be based in macro-cues, such as body

movements, body postures, and head orientations, and face-specific cues such as eye gaze. An investigation of general context signals is advantageous for determining what cues influence the behaviors of others and are available for predicting the behaviors of others, both vital for navigating social interactions. Whereas play-specific signals are often limited to the play context, general context signals may work to emphasize the social information contained in play-specific signals.

5.4. Gorilla play

The ontogeny of gorilla play progressively increases in social and structural complexity as the infant matures into adolescence and early adulthood. In the beginning months, all social contact for the infant is with the mother, therefore it follows that the first appearance of play at approximately 4-6 months of age is reciprocal mother-infant play and exploratory solitary play. This solitary play includes behaviors such as clapping and patting of the body, and the manipulation of objects in the surrounding environment. As the strength of the infant grows, so does the vigor with which it tests the mother and her appendages as play objects, e.g., hair pulling, patting, climbing, etc. (Fossey, 1979). Throughout maturation, the infant's social circle expands, as does the availability of potential playmates. The development of social play is a gradual process with peer approaching and visual exams beginning in the fifth month. Interactions with peers typically occur concurrently with motherly contact, although as the infant matures and spends more time out of its mother's reach, it explores other individuals as play objects. Schaller's detailed accounts of mountain gorilla play demonstrate that adult gorillas, particularly the silverback, exhibit a high tolerance for infant solitary play. In one example he observed,

This description of gorilla play is unavailable due to copyright restrictions.

From the time the infant finds peers as playmates, play continues to gradually increase in complexity as the infant becomes more secure with group members and the surrounding environment (Fossey, 1979; Hoff *et al.*, 1981). More physically demanding solitary behaviors, including tree climbing, swinging, and twirling, begin to first appear in the seventh month. The frequency of social play also begins to overtake that of solitary play. Social play includes both gentle and rough forms[6]. Gentle play includes behaviors such as tickling, gentle grappling, jumping, and gentle wrestling. Rough play includes more rigorous and acrobatic behaviors such as play fighting, twirling, chasing, pushing, stamping, and rolling, which are often punctuated by moments of non-activity where one behavior transitions to another. Schaller again observed,

This description of gorilla play is unavailable due to copyright restrictions.

[6] In the literature these are also sometimes called passive and active play depending on the body of research reviewed. For this thesis, the gentle/rough distinction is sufficient because the word "passive" actually connotes an inactive or not readily participating partner, which is substantially different in meaning than the description "gentle".

These types of behaviors in social play, especially ones used during rough play, require a high degree of reciprocity, cooperation and communication between partners. Schaller's example illustrates that many of the behaviors used during play can be observed in additional social contexts and some, such as the juvenile's forceful grabbing and pinning down of the infant, can be misconstrued as aggressive, yet the interaction continues playfully once the infant breaks free. Aside from the aforementioned play-specific behaviors or play signals, there may also be more subtle cues that drive a play interaction. The ability to recognize ambiguous stimuli, such as how close a partner is in proximity, the specific body orientation of a partner, or whether the partner is looking in the actor's direction, can in turn translate into a response that governs the progression of the interaction. Since juvenile play bouts are frequent, there are multiple opportunities to gain and hone the skills necessary to make sense of this social information, and these skills can be practiced liberally with multiple partners in a relatively safe and playful arena. This recognition of social cues may improve with age and social experience via social play so an individual becomes more adept, or behaviorally flexible (Fagen, 1981), at identifying and using certain cues to modify their behaviors.

6. Dissertation aims and objectives

The aim of this thesis is to investigate the use and effectiveness of general social cues that

are available to great apes to judge the attentional direction of conspecifics. This thesis consists of two distinct sections: an experimental section, in which the attentional information potentially contained in the eyes of great apes (with a special reference to the role of white sclera) is analyzed; and an observational section, in which the display and use of attentional cues by gorillas in a social play context is studied.

Influenced by a 2001 eye coloration study by Kobayashi and Kohshima, the first objective of this research, presented in Chapter 2, is to explore sclera coloration in great apes, particularly gorillas. Kobayashi and Kohshima (2001) hypothesized that the all-dark eyes of great apes act as gaze camouflage and minimally contribute to the relay of gaze information. This dark sclera coloration contrasts with the white sclera of humans, which instead functions to accurately display and enhance gaze direction for observers (Kobayashi & Kohshima, 2001). However, naturalistic observations of gorillas (*Gorilla gorilla*) indicate variability in sclera coloration, i.e., coloration ranging from human-like all-white sclera to all-dark sclera. In light of the proposed contrasting sclera functions, Chapter 2 is an inquiry into how the natural variability in great ape sclera coloration can be reconciled with the proposed gaze camouflaging and gaze enhancing hypotheses of Kobayashi and Kohshima and Tomasello *et al*. Delving further into this line of questioning, Chapter 3 explores the social information that is available in both human and non-human primate eye gaze. This chapter also evaluates the contribution of white sclera to the perception of gaze direction and detection using an experimental paradigm based on an illusory technique called the "Bogart illusion" (Sinha, 2000).

The second section of this thesis focuses on the role of attentional cues within gorilla play behavior. The majority of the primate social play literature focuses on the structure of general behavioral sequences of play-fighting, rough-and-tumble play, and the gaits used during play locomotion (Chalmers, 1984; Fagen, 1981, 1993; Hoff *et al.*, 1981; Pellis, 1997; Pellis & Iwaniuk, 2000; Pellis & Pellis, 1997, 2007). In particular, there has been an emphasis on how these general behaviors are put into practice for future serious contexts, e.g., determining the functionality of play. However, outside of the functional suggestion of the role of play signals, little research has been conducted to pinpoint how general behavioral cues are used to initiate, maintain, and terminate play bouts. This project aims to reconcile this gap in the literature and explore how gorillas use general cues, especially cues of direction of attention, to gauge the attention and intentions of playmates to successfully initiate, maintain, and/or terminate play.

Cues to the direction of attention, specifically eye gaze, head orientation, and body orientation, are available to gorilla play partners throughout play bouts and can occur in many combinations. Because visual information about objects and agents within the surrounding environment can be informative for engaging socially within that environment, it appears that periodically establishing and monitoring subsequent changes to these specific attentional cues could have a significant impact on the flow of play between gorilla partners. While some non-human primate research suggests that head and body orientation may be more efficient indicators of attentional direction in an ape partner, the potential role of different cues, including eye gaze, merits further evaluation. Chapter 4 examines the role of attentional cues used by captive western lowland gorilla

(*Gorilla gorilla gorilla*) partners within the dynamic social context of play. A novel time frame is introduced within play behavior, "vigilance periods", which are described as momentary transitional spans of time where gorillas pause from play with one another. Eye gaze, head orientation, and body orientation are explicitly evaluated during these novel time frames. Finally, Chapter 5 complements the preceding attention orientation analyses of Chapter 4 by examining the relationship between gorilla postures, behaviors, and movements that accompany the frequent and variable changes in attention cue orientations.

CHAPTER 2:

Gorillas with white sclera: a preliminary study of a naturally occurring variation in a morphological trait linked to social cognitive functions

Chapter 2: Gorillas with white sclera: a preliminary study of a naturally occurring variation in a morphological trait linked to social cognitive functions

Introduction

This quotation is unavailable due to copyright restrictions.

Coloration observations of extant primates have shown that as an order, primates come in a variety of coloration schemes. The majority of the coloration literature focuses on pelage and skin coloration, and typically these studies investigate coloration as it relates to sexual selection, concealment, aggression and dominance levels (Caro, 2005 & 2009). One such example includes the coloration changes that occur with maturation – male gorillas (*Gorilla gorilla*) experience a graying or silvering of the hair on the back, which is indicative of adulthood. In other instances, primate infants start out with conspicuous natal coat colorations that become less dramatic as the individual ages, e.g., the orange coat of an infant Silvery Leaf Monkey (*Trachypithecus cristatus*) [Bradley & Mundy, 2008; Treves, 1997]. The appearance of flamboyant natal coat colorations in primate infants appears counterintuitive for survival tactics, because brightly advertising the location of an infant could potentially draw unwanted attention from predators and aggression from group mates, e.g., infanticide from adult males. Alloparenting[7] from group mates has been suggested as one possible hypothesis for bright infant coats, although conclusive evidence substantiating this function has yet to be discovered (Bradley & Mundy, 2008; Treves, 1997). Other bright and highly visible colorations in

[7] Gerald *et al*. (2006) present results that female Rhesus macaques (*Macaca mulatta*) do not show a preference for infant face coloration. This provides opposing evidence for an alloparenting hypothesis, although additional empirical studies in other species are necessary.

primates often occur on the bare-skinned areas of both males and females, e.g., the bright red sexual swellings of female Hamadryas baboons (*Papio hamadryas*) in estrous, the bright blue genitals of male Vervet monkeys (*Chlorocebus pygerythrus*), and the red and blue banded face of the Mandrill (*Mandrillus sphinx*). These colorful advertisements highlight a seemingly contradictory relationship between sexual selection, which advertises mate quality and availability, and the more conservative survival qualities of natural selection, e.g., camouflaging.

The current literature contains few studies that specifically evaluate eye coloration in primates (iris color in *Macaca fuscata*: Zhang & Watanabe, 2007) with even fewer focusing on sclera coloration or eye morphology (Knapp *et al*., 2007; Kobayashi & Kohshima, 2001; Schmittbuhl *et al*., 1999). Interestingly, the Kobayashi and Kohshima (2001) study has been the only recent study with the specific focus of differentiating and categorizing extant primate eye coloration. Kobayashi and Kohshima used both quantitative measures, width/height ratios (WHR) and exposed sclera size indices (SSI), and qualitative measures, coloration comparisons of the iris, sclera, and surrounding facial skin, and determined that the morphological qualities of the human eye are unique from other extant primates. More explicitly, great ape eyes are described as all-dark, a dark iris and dark sclera, contrasting with human eyes, which have a dark iris set within a white sclera. Histological evidence establishes that the white sclera of humans is the result of a transparent conjunctiva and a sclera that lacks pigmentation. Non-human primate evidence, extrapolated for all primates from the examination of two macaque species, indicates that primates also possess an inner scleral portion that is white but has

pigmentation deposits in the epithelium cornea, conjunctiva, and sclera. Through WHR and SSI measurements, the study authors also determined that in comparison to non-human primates, human eyes are especially elongated in the horizontal direction, and direct gazes exposed a greater amount of visible white sclera. These morphological characteristics contribute to an enhanced overall visibility of gaze directions, and make the human eye one of the most easily recognized in comparison to extant primate relatives.

The coloration schemes presented in the Kobayashi and Kohshima study have become widely accepted within the current primate literature, especially within the comparative gaze-following research (*social gaze review*: Emery, 2000; Laube *et al.*, 2011; Provine *et al.*, 2011), as a key difference between humans and other primates. The attribute of white sclera has been suggested to be a gaze enhancing adaptation exclusive to humans, creating a "cooperative eye" that enhances gaze direction between communicating humans to convey important attentional information, especially during joint interactions ("*cooperative eye hypothesis*": Tomasello *et al.*, 2007). The simple dark and light coloration contrast, which could be quickly utilized by conspecifics, both enhances the visibility of the eyes within the face outline and specifically advertises eye gaze direction by amplifying iris visibility. This evolution of a white sclera trait, has been indicated to be a uniquely human adaptation (Kobayashi & Kohshima, 2001; Tomasello *et al.*, 2007), and suggests that the conveyance of gaze direction, through the attendance to eye gaze, is a highly used and important communicative channel for humans. The inverse conclusion has been drawn for the lack of a white sclera trait, and instead, all-dark eyes confer the

great apes a different gaze advantage, namely gaze camouflage. The advantages of concealing gaze direction from conspecifics have been discussed mainly within a competitive context; the concealment of eye gaze direction could aid in the avoidance of potential conspecific aggression or deceive conspecifics about interesting objects within the environment (Kobayashi & Kohshima, 2001; Tomasello *et al.*, 2007). However, minimal research has been conducted to lend support to this opposing hypothesis.

Based on the single eye coloration survey of Kobayashi and Kohshima, all great ape individuals are expected and assumed to adhere to this particular coloration scheme, barring any aberrant genetic mutations (e.g., albinism). However, casual observations of a number of great ape individuals, particularly gorillas (although certainly not restricted to), suggests that this expected uniformly dark eye may not be the universal rule, and that rather, degrees of color variation within the sclera might be relatively frequent and include individuals seemingly with a complete human-like white sclera (Fig. 1).

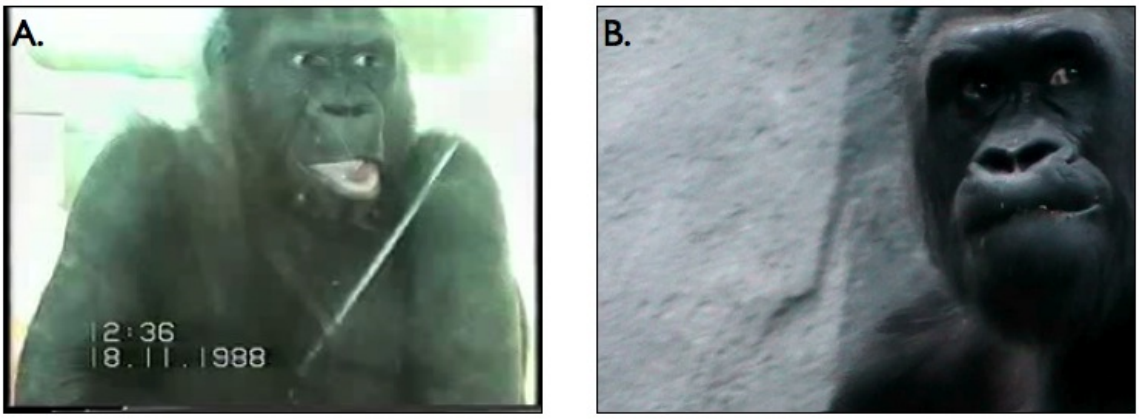


Fig. 1 – Two examples of gorillas with the white sclera characteristic: A) Nadia at the Madrid Zoo in Madrid, Spain (courtesy of Dr. Juan-Carlos Gómez) and B) Bana at the Brookfield Zoo in Chicago, IL (video still taken by JM).

The above examples illustrate that when these gorillas gaze laterally, the sclera visible to an observer is much lighter than either the iris or the surrounding facial skin. In Nadia's case (A), the sclera depigmentation in both her eyes has occurred to a degree where her eyes could be referred to as "human-like" and shows the coloration characteristics for human eyes described by Kobayashi and Kohshima. In Bana's case (B), the depigmentation of her left eye is heavier than her right eye but still prominently contrasts with the surrounding darkness of her face and hair. Do the eyes of these two individuals really conform to the human coloration pattern as defined by Kobayashi and Kohshima? If so, do they represent a minority trend within the gorilla population, which may have implications for an understanding of the evolution of a distinctive human eye coloration pattern, or are they simply unique, atypical examples of a morphological aberration? To further explore these questions, this study aimed to investigate the nature and extent that a lightened sclera characteristic can be observed in gorillas (*Gorilla gorilla*). To do so, I collected photographic samples of gorilla faces with different gaze directions, direct or averted, and analyzed them with the methods and measurements developed by Kobayashi and Kohshima (2001).

Methods

1. Study sample

This study examined 86 photographs, representing 81 individuals, of both western lowland (*Gorilla gorilla gorilla*) and mountain gorillas (*Gorilla beringei beringei*) that were collected from a variety of resources. Initially, several survey questionnaires were sent to zoos throughout the UK requesting the help from primate keepers to document the

presence of white sclera in their gorilla groups (K. Pullen, Paignton Zoo; J. Mansell, Belfast Zoo). Unfortunately, the return on the survey was much smaller than anticipated and the proposed project to survey eye coloration of the majority of gorillas housed within UK zoos had to be reassessed. To complement the survey return, online resources (via Google images) were consulted for high-quality images of gorilla faces that contained eyes that were sufficiently clear (non-pixilated) for analysis. Additionally, a photographic book documenting mountain gorilla group members was used to provide further examples of gorilla faces for the dataset (Eckhart & Lanjouw, 2008) [Table 1].

Photographs	Species	*n* individuals
Online (variety of sources)	*Gorilla beringei beringei*	**9**
	Gorilla gorilla	**16**
Zoo-housed individuals (UK zoo survey return and online sources)	*Gorilla gorilla gorilla*	**44**
Mountain gorilla book (Eckhart & Lanjouw, 2008)	*Gorilla beringei beringei*	**17**

Table 1 – The three photograph sources for gorilla faces and the number of individuals derived from each source categorized by species type.

Data were recorded using Microsoft Excel. When known, data on the photograph location, the name of the gorilla within the photograph, and species type (mountain or lowland) were obtained to avoid a repeated analysis of individuals. Gaze direction in relationship to the camera was also recorded as either direct or averted for further categorization purposes (Table 2).

Photograph Gaze Direction	*n* (no. of gorilla photographs)
Direct gaze	**27**
Averted gaze	**59**

Table 2 – Photographs of the gorillas categorized by gaze direction. Only four of the gorilla individuals within the dataset had two photographs to represent a direct and an averted gaze.

The reason for noting gaze direction differences was based on the observation that there was variability in the amount of exposed sclera depending on the position of the iris as it moved within the outline of the eye. A previous study of Bornean orangutans (*Pongo pygmaeus*) reported that an averted gaze, i.e., a laterally gazing individual, exposed as much visible sclera to a conspecific as a human direct gaze (Kaplan & Rogers, 2002)[8]. Fig. 1 illustrates that the white sclera characteristic is best recognized when the gorilla is gazing laterally. An analysis of direct and averted gazes in gorillas also allowed for this study to expand on the Kobayashi and Kohshima (2001) analyses, which only evaluated direct gazing primates. Further extending the analyses of the original study, this study also collected two photographs apiece of human individuals (n = 13 individuals) with a direct and averted gaze (n = 26 photographs).

2. WHR and SSI measurements

Each photograph was input into the NIH *ImageJ* program (1.45o, W. Rasband, National Institutes of Health, USA, http://imagej.nih.gov/ij), and the measurement tool was used to

[8] Bornean orangutans were also observed to use sideways gazing as the dominant method of gazing between conspecifics. This result, in combination with the increased visible sclera when sideways glancing, led the authors to disagree with Kobayashi and Kohshima's hypothesis that humans are better than the great apes at communicating via gaze direction, e.g., through the high visibility of the iris, and instead preferences for a particular type of gazing should be accounted for when drawing comparisons between gaze use in great apes and humans.

measure two parameters for both the left and right eyes individually, following the methods of Kobayashi and Kohshima (2001):

1) **Width/height ratio** (WHR): WHR was the calculation of A/B where A = the distance between the corners of the eye, including the vestigial portion of the nictitating membrane in the corner of the eye, and B = the longest perpendicular line between the top and bottom eyelids; and
2) **Exposed sclera size** (SSI): SSI was the calculation of C/D where C = the measurement of the width of the exposed eyeball, excluding the vestigial portion of the nictitating membrane in the corner of the eye, and D = the diameter of the iris (Fig. 2).

Fig. 2 – The measurements A-D were obtained for each eye of the photographs and represented, **top**: width/height ratio (A/B); and **bottom**: exposed sclera size (C/D) [video stills taken by JM].

WHR measurements estimated the relative elongation of the eye, and SSI measurements estimated the amount of visible sclera within the eyeball. These measurements provided

an estimate of the potential size and form of the contrast between the areas of sclera and iris within the eye. In each photograph, the dimensions A-D were measured three times for each visible eye (left and right), and the values were then averaged to reduce measurement uncertainty. These averages for both the left and right eyes were again averaged together to produce WHRs and SSIs for each photograph, which could then be further combined to find the mean WHRs and SSIs for both direct and averted gazing photographs.

3. Sclera coloration measurements

Although the different colorations between human and non-human primate eyes were a primary focus of the results of Kobayashi and Kohshima (2001), the authors did not provide a detailed quantitative analysis of these differences, which may have been because of the categorical nature of the color distinction they observed. The authors did however, report a relative gradation scale between the face, sclera, and iris colorations, which resulted in the classification of primates into four coloration types: 1) face ≅ sclera ≅ iris; 2) face < sclera ≅ iris; 3) face ≅ sclera > iris; and 4) face > sclera < iris. Since a preliminary inspection of my gorilla photograph dataset suggested that the white sclera characteristic might vary across a continuum, which would render the above classifications unsuitable to explain the variability within my dataset, it was necessary to conduct additional quantitative analyses.

The two main objectives of this portion of the measurements were to provide a quantification of the proportion of the eye that contained whitened sclera and to document the pigment degradation pattern (if any existed). Since no such study has thus

far been reported to provide guidelines for an empirical analysis, I had to develop my own methods to quantitatively analyze the patterns of pigment degradation in the sample of gorilla eyes. To better quantify the proportion of whitened sclera within the eye, a 0-10 scale was used (implemented by the study author JM and one other observer CF) to correspond with the observer's impression of the amount of visible sclera that was considered lightened. For example, if the eye had no visibly lightened sclera then it was given a score of 0, whereas an eye that had a completely white sclera was given a score of 10.

Additionally, six patterns of white sclera were defined to further categorize and represent pigment degradation of the eyeball. These sclera patterns were categorized as:

A) **All-dark sclera:** the sclera of the individual is completely dark and there is no visible depigmentation;
B) **"Patchy" pattern**: various areas of variable sizes are lighter than others;
C) **"Banded" pattern**: the lightened sclera appears as if it runs from the top eyelid to the bottom eyelid in a columnar shaped band and is typically (but not always) positioned between two darker bands or areas of sclera;
D) **"Crescent" pattern**: the lightened sclera forms a half moon shape where there is less depigmentation around the middle edge of the iris (darker region) and more depigmentation at the iris poles (lighter regions);
E) **Combination pattern**: two of the above patterns are present; or
F) **All-white pattern**: the sclera of the individual is completely lightened.

This illustration of gorilla sclera patterns is unavailable due to copyright restrictions.

Fig. 3 – Pictorial representations of the white sclera patterns: **A)** all-dark sclera; **B)** patchy; **C)** banded; **D)** crescent; and **E)** all-white sclera. A combination of patterns may also be observed, and patterns may vary in the left and right eyes of the individuals.

4. Inter-observer reliability

Inter-observer reliability was assessed for gaze direction (direct versus averted) and sclera coloration measurements (0-10 lightened sclera proportion scale and white sclera patterns). To assess gaze direction reliability, a primary (JM) and secondary coder (CF) independently scored the gaze directions (direct or averted) of both the gorilla (n = 86) and human (n = 26) photographs. In gaze direction judgments, inter-observer reliability was rated as being in nearly perfect agreement with a Cohen's kappa value of k = .830 (p < .001). To assess the sclera coloration measurements, the secondary coder (CF) scored each eye in each photograph (n = 224) on the 0-10 scale for lightened sclera. The inter-observer reliability was rated as being in substantial agreement with a Spearman's

correlation value of $r = .980$ ($p < .001$)[9]. Inter-observer reliability was rated as in nearly perfect agreement with a Spearman's correlation value of $r = .918$ ($p < .001$) for the white sclera pattern judgments ($n = 224$).

Results

When a width/height ratio (WHR – eye elongation measure) and amount of exposed sclera size (SSI) could be measured (WHR, $n = 78$; SSI, $n = 68$), the gorilla photographs were additionally categorized by gaze direction (direct or averted) for a more accurate comparison to the Kobayashi and Kohshima (2001) WHR and SSI results. Their original study analyzed WHR and SSI values for only direct gazing primates; therefore, a comparison could only be made between the original direct gazing values for gorillas and humans and the following direct gazing values.

1. Direct gaze WHR and SSI measurements: gorilla and human eyes

A preliminary evaluation of the direct gazing mountain (*Gorilla beringei*) and lowland (*Gorilla gorilla*) species revealed no significant differences between the WHR means (*mountain* WHR = 1.86 ± 0.29; *lowland* WHR = 2.02 ± 0.29; *independent samples t-test*: $t_{(27)} = -1.296$, $p > .05$) or SSI means (eyeball/iris proportions) [*mountain* SSI = 1.67 ± 0.25; *lowland* SSI = 1.64 ± 0.35; *independent samples t-test*: $t_{(22)} = .136$, $p > .05$]. Direct gazing gorilla WHR and SSI data from both species were therefore temporarily combined for comparison to the original study results. This study observed an overall mean WHR (± *SD*) = 1.98 ± 0.29 ($n = 29$, WHR range = 1.4-2.7) for direct gazing gorillas. This

[9] Observer responses were assessed on an ordinal scale (0-10) and were shown to be within ≤ 1 degree of agreement in 93.7% of responses (e.g., observer 1 responded with a value of 6 and observer 2 responded with a value of 7).

WHR value was similar to the WHR value presented by Kobayashi and Kohshima (*n* = 4, WHR = 1.9, WHR range = 1.8-2.1). Similarly, the overall SSI values of this study (*n* = 24, SSI = 1.65 ± 0.32, SSI range = 1.2-2.37) were similar to the SSI values of the original (*n* = 4, SSI = 1.75, SSI range = 1.5-1.9) [Table 3].

	Kobayashi and Kohshima (2001) study	**Current study**		
		Gorilla beringei	*Gorilla gorilla*	Gorillas (overall)
Width/height ratio (**WHR**)	1.9	1.86 ± 0.29	2.02 ± 0.29	1.98 ± 0.29
Exposed sclera size index (**SSI**)	1.75	1.67 ± 0.25	1.64 ± 0.35	1.65 ± 0.32

Table 3 – The mean width/height ratio (± *SD*) and exposed sclera size (± *SD*) values reported for direct gazing gorillas comparing the original and current studies.

An evaluation of direct gazing human eyes observed a mean WHR = 3.24 ± 0.49 (*n* = 13, WHR range = 2.6-4.4), which was higher, but roughly consistent with the WHR range reported for direct gazing human eyes in the original study (*n* = 659, WHR ≅ 2.9, WHR range = 2.4-3.2). The mean SSI values observed in this study *(n* = 13, SSI = 1.82 ± 0.13, SSI range = 1.5-2.1) were more consistent with the SSI values observed in the original (*n* = 659, SSI = 1.9, SSI range = 1.7-2.1) [Table 4].

	Kobayashi and Kohshima (2001) study	**Current study**
	Humans	*Humans*
Width/height ratio (**WHR**)	2.9	3.24 ± 0.49
Exposed sclera size index (**SSI**)	1.9	1.82 ± 0.13

Table 4 – The mean width/height ratio and exposed sclera size (± *SD*) values reported for direct gazing humans in both the original study and this study.

A comparison of direct gazing WHRs observed a significant difference among species

type (*one-way ANOVA*: $F_{(2,39)} = 54.609$, $p < .001$) and Tukey's *HSD* determined that the mean WHR of humans was significantly higher (3.24 ± 0.49) than the mean WHR for either lowland or mountain gorillas (*lowland* = 2.02 ± 0.29; *mountain* = 1.86 ± 0.29) [Table 6]. A comparison of direct gaze SSI means observed no significant differences between the species ($F_{(2,34)} = 1.654$; $p > .05$); the SSI values were similar for direct gazing humans, mountain and lowland gorillas.

Overall, the results for direct gazes in gorillas replicated, with a larger sample size, the results for direct gazing gorillas originally reported by Kobayashi and Kohshima. The significant difference between mean human and gorilla WHRs suggests a difference between human and gorilla eye shape with an elongation of the human in the horizontal direction. However, the SSI ratios were not significantly different between direct gazing human and gorilla stimuli, although there was a tendency for human SSI to be slightly larger. This result contradicts the Kobayashi and Kohshima result that human SSI is higher than other species of Hominidae.

2. Averted gaze WHR and SSI measurements: gorilla and human eyes

The same WHR and SSI measurements were obtained from averted gazing eyes, and a species comparison again observed significant differences in the WHR values between averted gazing humans, mountain, and lowland gorillas (*one-way ANOVA*: $F_{(2,59)} = 58.567$; $p < .001$). A Tukey's *HSD* determined that again, averted gazing humans had a mean WHR (2.94 ± 0.40) that was significantly higher than either lowland or mountain gorilla mean WHRs (*lowland* = 2.21 ± 0.28; *mountain* = 1.77 ± 0.19). Interestingly,

lowland gorillas were observed to have a significantly higher WHR than mountain gorillas (*lowland* = 2.21 ± 0.28; *mountain* = 1.77 ± 0.19). A comparison of averted gazing SSI means observed no significant difference between humans, mountain, and lowland gorillas ($F_{(2,54)} = 2.376$; $p > .05$), although lowland gorillas had the highest SSI mean (Table 5). In particular, the proportion of exposed sclera in averted gazing gorilla and human eyes was similar. This was similar to the result for direct gazes in which the proportion of exposed sclera was similar in all three species. Overall, when WHR and SSI measurements (Kobayashi & Kohshima, 2001) are applied to averted gorilla eyes, the SSI parameter (the estimate of exposed sclera) changes and is comparable to the human eye.

	Humans	*Gorilla beringei*	*Gorilla gorilla*
Width/height ratio (**WHR**)	2.94 ± 0.40*	1.77 ± 0.19*	2.21 ± 0.28*
Exposed sclera size index (**SSI**)	2.07 ± 0.16	1.95 ± 0.35	2.21 ± 0.47

Table 5 – Species comparison of mean width/height ratio (± *SD*) and exposed sclera size (± *SD*) values in averted gazing gorillas and humans. Significant differences (*) were observed between the averted WHR values for all species types.

3. Averted vs. direct gazes: species comparisons

No significant differences were observed for the WHR means between direct and averted gazing humans (Table 7). This non-significant result was the same for WHR means between direct and averted gazing mountain gorillas. However, averted gazing lowland gorillas exhibited a significant increase in WHR mean (*direct gaze*: $n = 21$, WHR = 2.02 ± 0.29; *averted gaze*: $n = 33$, WHR = 2.21 ± 0.28; $t_{(52)} = -2.400$, $p = .02$). The SSI means were higher for averted gazes than direct gazes in all three species; however, only human

($t_{(24)}$ = -4.339, p < .001) and lowland gorillas ($t_{(44)}$ = -4.337, p < .001) exhibited significant results (mountain gorillas were near significant: $t_{(20)}$ = -1.934, p = .067).

4. White sclera colorations: gorilla photographs

Both direct and averted gazes of all three species were analyzed to determine how much of the visible sclera contained depigmentation (on a scale of 0-10). A score of 0 indicated that the sclera had no visible depigmentation and was "all dark" whereas a score of 10 indicated that the sclera was devoid of any color and was "all white". Assessments were obtained for both the left and right eyes with each individual contributing two eyes to the overall *n* value. All human eyes, both direct and averted gazing, ranked a 10 on the 0-10 scale because they all contained sclera that was completely white (*n* = 52 eyes, 100% had complete depigmentation). In direct gazing mountain gorilla eyes (*n* = 14 eyes), 14.3% of the eyes contained visible depigmentation, whereas 68.4% of direct gazing lowland gorilla eyes contained visible depigmentation (*n* = 38) [Fig. 4, top]. The proportion of visible depigmentation in the sclera increased in both averted gazing mountain (*n* = 40, *depigmentation* = 57.5% of eyes) and lowland gorillas (*n* = 76, *depigmentation* = 90.8%) [Fig. 4, bottom].

	Kobayashi & Kohshima (2001) study		**Current study**		
	Humans	*Gorillas*	*Humans*	*Gorilla beringei*	*Gorilla gorilla*
Width/height ratio (**WHR**)	2.9	1.8 - 2.1	3.24 ± 0.49*	1.86 ± 0.29	2.02 ± 0.29
Exposed sclera size index (**SSI**)	1.9	1.5 - 1.9	1.82 ± 0.13	1.67 ± 0.25	1.64 ± 0.35

Table 6 – The mean width/height ratio (± *SD*) and exposed sclera size (± *SD*) values reported for direct gazing humans, mountain, and lowland gorillas. Significant differences (*) were observed between the mean WHR value for humans in comparison to both mountain and lowland gorilla mean WHRs but not for SSI.

	Humans		**Lowland gorillas (*Gorilla gorilla*)**		**Mountain gorillas (*Gorilla beringei beringei*)**	
	Direct gaze	**Averted gaze**	**Direct gaze**	**Averted gaze**	**Direct gaze**	**Averted gaze**
Width/height ratio (**WHR**)	3.24 ± 0.49*	2.94 ± 0.40	2.02 ± 0.29*	2.21 ± 0.28	1.86 ± 0.29	1.77 ± 0.19
Exposed sclera size index (**SSI**)	1.82 ± 0.13*	2.07 ± 0.16	1.64 ± 0.35*	2.21 ± 0.47	1.66 ± 0.25	1.95 ± 0.35

Table 7 – The overall width/height ratio (± *SD*) and exposed sclera size (± *SD*) results for direct and averted gazes categorized by species. Significant differences (*) were observed for the WHR and SSI values between direct gazing and averted gazing species.

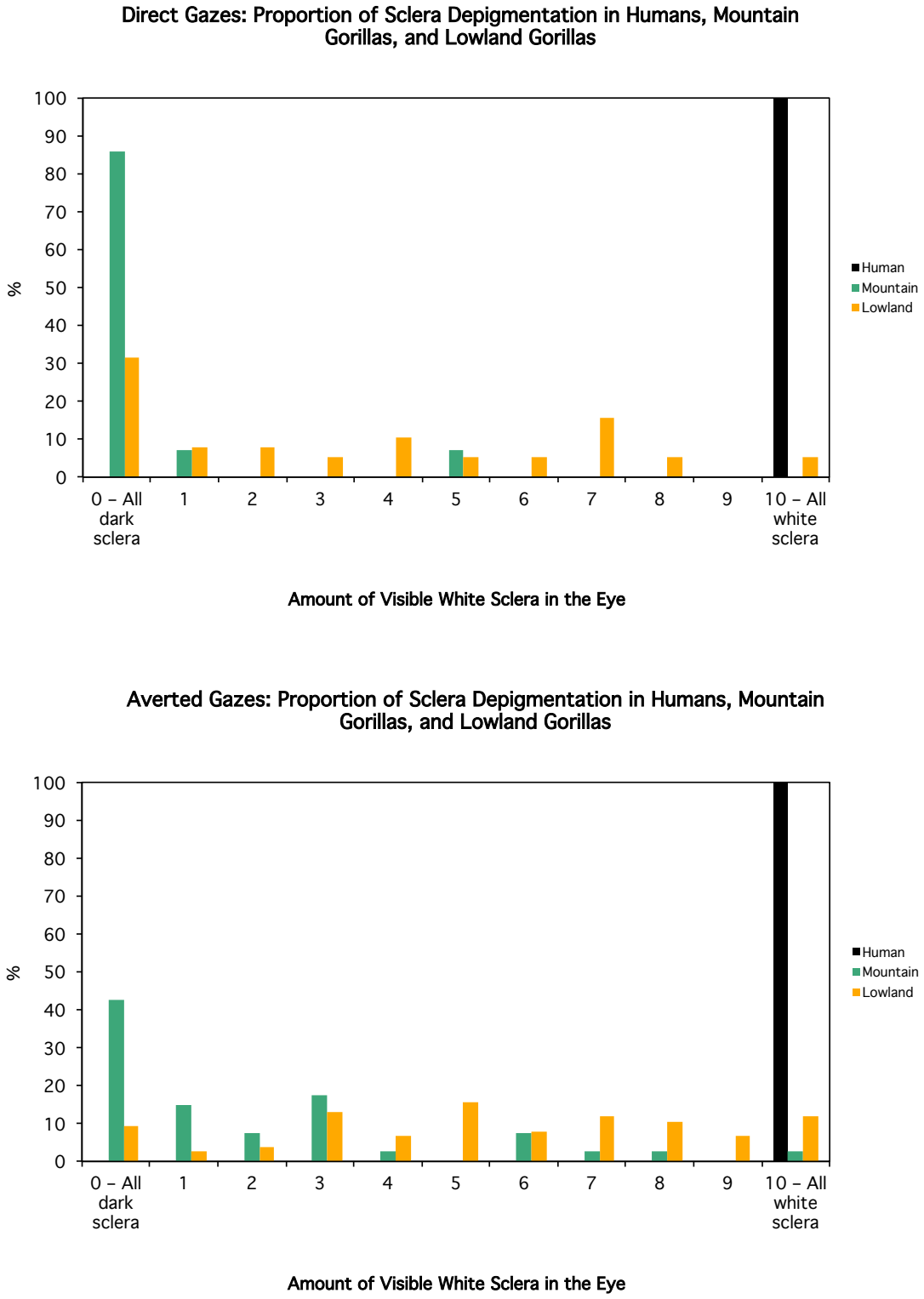


Fig. 4 – The observed proportions of sclera depigmentation for direct gazing (**top**) and averted gazing (**bottom**) human, mountain gorilla, and lowland gorilla eyes. The eyes were assessed using a white sclera scale (0-10).

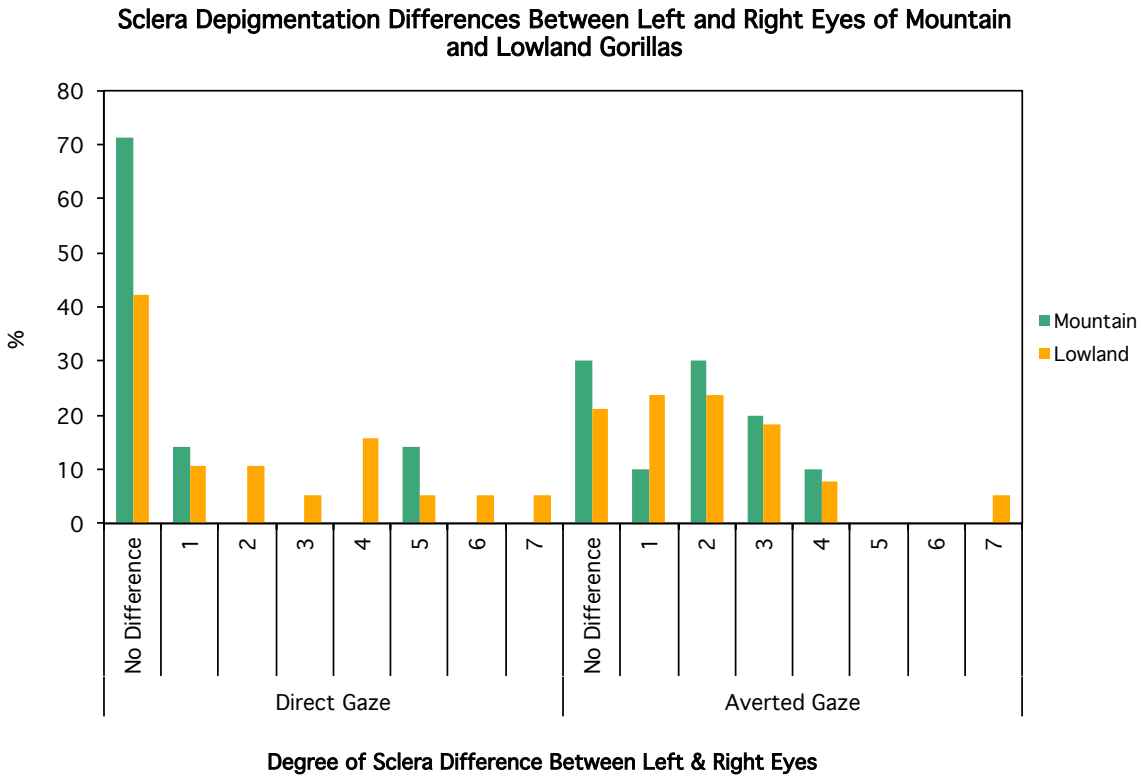


Fig. 5 – A comparison of the degree of sclera coloration difference between the left and right eyes of both direct and averted gazing mountain and lowland gorillas. Direct gazing mountain gorillas typically exhibited no degree of sclera difference between the left and right eye (71.4%), which contrasted to the more variable sclera differences observed for direct and averted gazing lowland gorillas.

Typically, direct gazing mountain gorillas (71.4% of individuals) were judged to have similar amounts of pigment degradation (on the 0-10 scale) in each eye (Table 8). Direct gazing lowland gorillas more frequently had one eye that exhibited more depigmentation than the other by ≥ 1 degree on the 0-10 scale (57.9% of individuals). Averted gazing mountain and lowland individuals more frequently possessed sclera that differed from one another by ≥ 1 degree (*mountain* = 70.0% of individuals; *lowland* = 79.0%).

Scale difference between left and right eye sclera coloration	Mountain Gorilla		Lowland Gorilla	
	Direct (%)	Averted (%)	Direct (%)	Averted (%)
No difference (0)	71.4	30.0	42.1	21.0
1	14.3	10.0	10.5	23.7
2	-	30.0	10.5	23.7
3	-	20.0	5.3	18.4
4	-	10.0	15.8	7.9
5	14.3	-	5.3	-
6	-	-	5.3	-
7	-	-	5.3	5.3

Table 8 – The degree of difference between left and right sclera colorations observed for direct and averted gazing mountain and lowland gorillas.

White sclera patterns were then assessed in each eye. In mountain gorillas, both direct and averted gazing individuals most frequently had eyes that contained an all-dark sclera pattern (53.7% of eyes) [Table 9]. This contrasted with lowland gorillas that exhibited an overall mixture of white sclera patterns that were visible in both direct and averted gazes.

White sclera pattern	Mountain Gorilla (%)		Lowland Gorilla (%)	
	Direct	Averted	Direct	Averted
All-dark sclera	85.7	42.5	31.6	9.2
Patchy	7.1	25.0	18.4	21.0
Crescent	7.1	10.0	23.7	22.4
Banded	-	15.0	5.3	21.0
Combination	-	5.0	15.8	14.5
All-white sclera	-	2.5	5.3	11.8

Table 9 – The categories of white sclera patterns observed in mountain and lowland gorilla eyes categorized by the two gaze types.

Discussion

This study sought to expand on the original eye coloration study conducted by Kobayashi and Kohshima (2001) in two ways: 1) by expanding the gorilla sample size analyzed in the original study (n = 4) to reassess the original quantitative eye measurements and the stringent eye coloration conclusions put forth by the original study authors; and 2) by introducing a contrast evaluation between direct and averted gazing eyes in the eye morphology measurements because the original study had been limited to the analysis of direct gazing eyes.

The WHR and SSI values observed for direct gazing gorillas of this study support the conclusion of Kobayashi and Kohshima that the morphologies of gorilla and human eyes are different, but only in some respects. My results suggest that the human eye is morphologically different from the gorilla eye, but only in the elongation of the eye (as measured by the WHR index) rather than the total amount of sclera exposed, as was originally suggested by Kobayashi and Kohshima. More specifically, humans have a greater WHR, which horizontally elongates the eye outline. Contrasting with Kobayashi and Kohshima, this study showed no significant difference in the SSI measurement that estimates the amount of exposed sclera in the human and gorilla eye.

In their results, Kobayashi and Kohshima proposed that the elongation of the human eye and the larger amount of visible sclera were both the result of an adaptation to a terrestrial lifestyle; the increase in a WHR would allow for increased eyeball movement extending the visual field in the horizontal plane. The authors suggest that increased eyeball

movement, via increased WHR and SSI, has not only functional properties for the individual collecting visual information about the environment, but also has gaze signaling properties. The authors suggest that both of these modified morphological features in humans would be particularly useful to a conspecific when they are presented with a direct gazing eye, and the increased contrast between visible sclera and iris would also increase the direct gaze signal. My results suggest that it is the elongated eye feature that more reliably distinguishes the human eye from the ape eye (as represented by gorillas in this study) and even if the amount of exposed sclera remains roughly the same, the elongation of the human eye would make the advertisement of gaze direction easier (on the horizontal plane) by providing a more reliable contrast signal.

Extending beyond the original Kobayashi and Kohshima evaluation of only direct gazes, this study also incorporated novel analyses that examined humans and gorillas engaged in averted gazes. A difference in eye elongation (WHR) between humans and gorillas was also observed in averted gazing eyes, which confirms the importance of this morphological difference. In both humans and gorillas, averted gazing individuals possessed larger mean SSIs than their direct gazing counterparts. My results of an increased SSI in averted gazing gorillas are consistent with similar results for a larger averted gazing SSI in Bornean orangutans (*Pongo pygmaeus*) [Kaplan & Rogers, 2002]. Overall, these larger SSI values for averted gazes can be attributed to the morphology of the eye in an averted condition; as the iris moves laterally within the eyeball, the amount of visible sclera on one side of the eyeball increases as the sclera on the other side, the side that the iris travels toward, decreases. This differs from a direct gazing eye where

the iris is centered within the eyeball and occupies the majority of the visible eye. The inclusion of averted gazing individuals also revealed an interesting difference between human and gorilla gazes: the increased SSI of an averted gazing gorilla was comparable to both direct and averted human SSIs. In other words, an averted gazing gorilla eye displays the same amount of visible sclera (or more in the case of lowland gorillas) as either a direct or an averted human gaze.

This species comparison suggests that the morphological changes of the human eye may have developed to specifically enhance the signaling value of direct gazes more than other gaze types. This evidence would be consistent with the current eye gaze literature that indicates that human infants orient toward and increase looking times, i.e., prefer to look, at conspecific eyes that are directed toward them (Farroni *et al*., 2002). It would also be consistent with the suggestion that direct gaze may serve special communicative functions, such as signaling communicative intent and displaying and detecting *ostension* (Gómez, 1996 & 2007). The authors of the cooperative eye hypothesis suggest that the understanding of communicative intentions may be particularly complex, or possibly unique to humans (Tomasello *et al*., 2007). A morphological change to facilitate the display of a direct gazing eye might have occurred in evolution with an increase in the importance of the use of ostensive signals. Although my results do not support that the elongation of the human eye was accompanied by an increase in the proportion of exposed sclera, it is still arguable that this change – that it increases the area of horizontal contrast between iris and sclera – was accompanied by a white sclera adaptation to further enhance the iris contrast and facilitate direct gaze communicative functions.

My study observed that the assumption that the sclera coloration of human and ape eyes are categorically different might not be entirely warranted. Although a proportion of my study's gorillas adhered to the all-dark eye coloration scheme (attributed by Kobayashi and Kohshima to all gorillas), not all did. Up to 90% of the lowland gorilla specimens in this study showed some degree of depigmentation and up to 12% showed complete white sclera in averted gazes. All-dark eyes accounted for less than one-third of the individuals examined and as little as 9.2% of averted gazing gorillas.

I observed an important difference between assessing direct gazes and averted gazes in gorillas. The "classic" all-dark sclera coloration pattern was more prevalent when evaluating direct gazing gorillas (*mountain* = 85.7%; *lowland* = 31.6%) than averted gazing gorillas (*mountain* = 42.5%; *lowland* = 9.2%). This result may have related to the overall smaller SSI for direct gazing gorillas and thus, the overall smaller amount of visible sclera. In averted gazing gorillas, the larger amount of visible sclera must have contributed to the visibility of any lighter sclera areas.

In general, the majority of the gorillas analyzed in this study were observed to possess varying degrees of sclera depigmentation; therefore, this study demonstrates that the casual observations of white sclera in gorillas, that originally initiated the study, were not isolated cases but instead appear to be a trend in a number of gorilla individuals. Without the application of a more systematic study of both captive and wild populations, the actual prevalence of white sclera cannot be accurately estimated in gorillas; however,

these results do demonstrate that the coloration schemes put forth by Kobayashi and Kohshima are not categorically accurate. This study was able to identify six sclera patterns for gorillas, but more research is necessary to investigate the extent of these and other potential patterns within the species.

The result of a natural variability in the degree that white sclera occurs in the great apes emphasizes that sclera coloration is not a simple all-or-nothing phenomenon as has been previously suggested. Therefore, the suppositions based for both humans and the great apes under the notion that sclera color is uniform within the species should be reevaluated. In particular, sclera variability in gorillas contradicts the proposed strict "gaze camouflaging" function proposed for ape eyes (Kobayashi & Kohshima, 2001). Natural selection should have eliminated the presence of white sclera in gorillas if it conferred significant disadvantages; however, its preservation in gorillas suggests that possessing a white sclera may not confer any significant disadvantages to gorillas. Simultaneously, the lack of preferential selection suggests that white sclera does not confer significant advantages to gorillas either. Therefore, my results oppose one portion of the cooperative eye hypothesis: gorillas, and perhaps other apes, do not have dark sclera as an adaptation to camouflage their gaze direction.

In summary, this study demonstrates that white sclera is not exclusively a human characteristic, and therefore the more relevant and uniquely adaptive characteristic of the human eye may in fact be its horizontal elongation. This elongation of the eye made white sclera an optimal background to promote iris direction, particularly advantageous

in an arena of communicative and cooperative social pressures. Not only would highly visible gaze-following be ecologically useful, but visible direct eye contact between two individuals also ostensibly "…express[es] and assess[es] communicative intent…" (Gómez, 1996). In this sense, the horizontal elongation of the eye in humans may allow for more complex communication via direct gazing that does not hold the same value for the great apes, which lack an elongation comparable to humans. It is possible that for the great apes, direct gazing is not the preferred or most ecologically relevant method of eye gaze communication. The previous result that Bornean orangutans prefer to use sideways gazing when viewing conspecifics (Kaplan & Rogers, 2002) coupled with the result that great ape averted gaze SSI is larger than a direct gaze SSI suggests that perhaps an averted gaze is more suitable for great ape eye gaze communication. However, gazing techniques and preferences in the great apes still require further investigation.

Ultimately, this study was not an evaluation of the frequency in which light sclera is present in gorillas, rather, it was an acknowledgement that sclera variability exists and was a preliminary examination into the morphological patterns observed. To further evaluate sclera variability in the great apes, the following chapter addresses questions concerning how a light versus dark sclera contributes to determining gaze direction in a conspecific. This has been assumed to be an inevitable enhancing effect of light sclera, but it has to my knowledge never been tested empirically.

CHAPTER 3:

White sclera as a cue of gaze direction: how humans perceive ape gaze with and without white sclera

Chapter 3: White sclera as a cue of gaze direction: How humans perceive ape gaze with and without white sclera

Introduction

A cursory comparison of the faces of modern day humans and extant apes reveals marked differences, such as the pronounced brow ridges and zygomatic arches of apes and superficial coloration differences of the skin, hair, and eyes. The orbits of modern humans and *Pan* are characterized by an elliptical elongation, which differs from the quadrangularity of the orbit of *Gorilla* (Schmittenbuhl *et al*., 1999). The adaptive morphological changes to the orbital region in anthropoids have been suggested to increase visual acuity, and variabilities have also been distinguished between nocturnal and diurnal species (Ross & Kirk, 2007). Aside from the anatomical changes to the eye that have enhanced primate visual acuity, ostensible coloration differences exist, particularly in human eyes, which are characterized by a dark iris and prominent white sclera. One result of Chapter 2 demonstrated that humans have also experienced a horizontal elongation in comparison to gorillas (characterized by a larger width/height ratio), which increases the amount of visible sclera and further enhances the visible contrast between the light and dark regions of a direct gazing eye (Kobayashi & Kohshima, 2001; Tomasello *et al*., 2007).

According to Kobayashi and Kohshima (2001), 85 of the 92 species of non-human primates evaluated in their study were classified as having a brown or dark brown sclera based on pigment deposits in the conjunctiva, sclera, and epithelium cornea (see Knapp *et al*., 2007 for a histological study of the gorilla eye). A study of a subset of 82 of these

primate species determined that 80 species had relatively homogenous colorations of the iris, the sclera and the surrounding face denoted by the authors as a Type 1 or Type 2 coloration. Type 1 primates had a nearly equal coloration of the iris, sclera, and skin (e.g., bonobos and gorillas) and Type 2 primates had a nearly equal coloration of the iris and sclera that were darker than the surrounding skin (e.g., chimpanzees and orangutans). Great apes of either coloration category have similarly dark irises and sclera, which was argued by the authors to decrease the ability to discern the outline of the iris. Such ambiguity of the iris placement led to the suggestion that this dark-on-dark coloration of the great apes acts as a camouflage that shields gaze direction from potential predators or conspecifics rather than promoting it (Kobayashi & Kohshima, 2001, 2010; Langton *et al*., 2000). In contrast, the white sclera of humans (Type 4 coloration) makes the iris more salient, which enhances the potential for displaying eye gaze direction.

However, the Kobayashi and Kohshima (2001) study was conducted based on the assumption that the examples of primate eyes that were evaluated were representative of each species; more specifically, that all gorillas belong to a Type 1 coloration category with a dark sclera and iris. However, the results of Chapter 2 demonstrate that a proportion of gorillas maintain variability in the depigmentation of the sclera, and therefore present a challenge to the proposed gaze camouflaging function of an all-dark eye. However, no such studies have examined the costs and benefits between dark and light sclera, and thus far, the "gaze camouflage" hypothesis has yet to be tested.

1. The cooperative eye hypothesis

As an extension of Kobayashi and Kohshima's (2001) study, Tomasello *et al*. (2007) were led to question the potential benefits that a pair of visible eyes would confer to humans. One such suggestion is that white sclera is a potential indicator of good health in an individual, and good health typically signals good genes and accordingly, a valuable mate (Tomasello *et al.*, 2007). However, to my knowledge, this hypothesis has not yet been explored. The authors presented another hypothesis, the "cooperative eye hypothesis", which posits that such a salient contrast evolved in humans within a context of pressures of enhanced cooperative-communicative abilities. These abilities relied on mutual social interactions between individuals and involved activities emphasizing joint attention and visually based communication (e.g., pointing). An individual who can quickly judge the attentional state of another has an adaptive advantage, particularly if they are the focus of that attention (Gómez, 1996; Langton *et al*., 2000; Tomasello *et al.*, 2007).

To systematically test the specific gaze cues used for judging the attentional direction of another, Tomasello *et al*. (2007) tested both human infants (20 12-month-olds and 20 18-month-olds) and 19 great apes (11 chimpanzees, 4 bonobos, and 4 gorillas). Orangutans were also tested; however, they failed to "attend" to gaze cues sufficiently enough to be scored and were excluded from the study. Six experimental conditions were used to investigate the contributions of gaze information from the eyes and head on the gaze-following abilities of the participants. These conditions consisted of: 1) *head only*: the experimenter closed their eyes and looked toward the ceiling with their head; 2) *eyes*

only: the experimenter kept the head stationary and only used the eyes to look toward the ceiling; 3) *both*: the experimenter used both the head and eyes to look toward the ceiling; 4) *neither*: the experimenter stared at the subject; 5) *back of head*: the experimenter sat with their back to the participant and looked with the head and eyes toward the ceiling; and 6) *back control*: the experimenter sat with their back to the participant and did not move.

Overall, the authors observed that both great apes and human infants used head and eye cues to follow an experimenter's "gaze" direction; however, a difference in eye and head cue use between the two species was observed (Tomasello *et al.*, 2007). The apes appeared to use head cues more frequently than the humans because they responded to the experimenter's gaze in the *head only* and *back of head* conditions. However, human infants responded less frequently to the *head only* condition and more frequently when the experimental condition involved the eyes; a result consistent with previous studies on infant gaze (Emery, 2000; Farroni *et al*., 2002; Rigato *et al*., 2010). The ape participants were also observed to distinguish between the front and back of an experimenter's head, as was determined by the more frequent response in the *back of head* condition versus the *back control* condition. This led the authors to suggest that the salient gaze cue used by the apes was the presence of the face. Tomasello *et al*. (2007) further suggested that because infants use available eye gaze information more frequently, the gaze information contained in human eyes would hold greater importance than the gaze information contained in more gross body parts such as the head and body. The authors reasoned that modern humans may have evolved a particular sensitivity to gaze information from the

eyes, and a dark/light contrast in the eyes would maximize the projection of information that could enhance cooperative contexts. Conversely, the lack of light sclera in the great apes generates the assumption that great ape eyes with dark sclera do not contain useful gaze direction information and great apes must rely on available head and body cues to determine the gaze direction of conspecifics. Yet, both *Pan* and *Gorilla* live in socially intimate groups with defined social hierarchies and engage in interactions that often involve complex behavioral sequences between proximal individuals (e.g., play behavior) [Harcourt, 1979; Schaller, 1963]. Why then, would gaze camouflage be a beneficial proposed function for dark sclera? Similarly, why should a light sclera enhance gaze direction perception?

2. Luminance cues enhancing the display of gaze

Information regarding the iris position within the eyeball can be extracted based on geometrical properties of the eye, such as the comparison of the relative locations of the outlines of the eyelid and iris (Anstis *et al*., 1969; Gibson & Pick, 1963). Eye luminance may also be a valuable and more easily perceptible cue for humans when determining the gaze direction of conspecifics. Darkening one side of the sclera has been shown to shift a participant's perceived direction of gaze based on a comparison of the luminance of both sides of the sclera (Ando, 2002) or the sclera and surrounding face (Ando, 2004). Various polarity contrast studies have demonstrated that reversing the polarity of the eyes or face (making the light areas dark and vice versa) causes inaccurate judgments and perceived reversals of gaze direction, thus underlining the importance of local eye information (Olk *et al*., 2008; Ricciardelli *et al*., 2000; Sinha, 2000; Tipples, 2005). Human infants have been shown to prefer positive polarity upright faces over any

negatively configured naturalistic or schematic face (Farroni *et al*., 2005), and adults have been shown to be less sensitive to any modifications of facial features when the changes are presented in negative polarity (Kemp *et al*., 1990).

3. The Bogart illusion

The "Bogart illusion" (Sinha, 2000), demonstrated using human observers, is one such simplistic polarity reversal study that illustrates how the human visual system may make use of a luminance cue to quickly judge the gaze direction of other individuals. Ten human participants were asked to judge the gaze direction of 8 photographic full human faces looking either to the left or right. The photographs were black-and-white and the prototype was a photo of actor Humphrey Bogart (Fig. 6) from which the effect took its name. The participants were 100% accurate when judging the gaze direction of the positive polarity photographs. A polarity inversion of the photographs exchanged the light and dark areas and generated the illusion that the photograph subject was gazing in a direction opposite to the original. The perception of this gaze reversal by the observer was reported 60-80% of the time. One suggestion for these results was that when assessing another individual for gaze specific information, humans operate on the assumption that the darkest part of the eye is the iris and therefore the part that "does the looking". The observer can then use such an ordinal brightness system to quickly judge the gaze direction of others. This ordinal brightness system would be particularly useful in lieu of geometric and morphological cues, such as an iris outline and nose direction, which may take longer to process and do not always hold up under inadequate viewing

conditions or at a distance[10]. Nonetheless, such luminance relationships would be expected to vary depending on the amount of contrast present in the eye that is being observed.

This image of Humphrey Bogart is unavailable due to copyright restrictions.

Fig. 6 – The black-and-white photograph of Humphrey Bogart, from which the "Bogart illusion" name derived.

4. Study aims and hypotheses

The aim of this study was to use the light sclera variability observed in great apes, and introduced for gorillas in Chapter 2, to assess the extent (if any) that light sclera contributed to gaze direction detection. Examples of human and naturally occurring extant dark and light sclera great ape eyes were used in the following contrast reversal experiments and explored whether: **1)** non-human great ape eyes with dark sclera actually

[10]Jenkins (2007) presents a counter-example using two images of the same face gazing in opposite lateral directions, one passed through a low Gaussian filter (9 cycles per image width) and the other through a high Gaussian filter (13.3 cycles per image width). The eyes of the final combined face, when viewed at a distance of 40-50 cm, appear to gaze in one direction but on increased distance from the stimulus (beyond 3 m) appear to gaze in the opposite direction. Jenkins suggests that competing geometric cues override luminance cues when judging gaze direction at close range.

lacked useful gaze information, in accordance with the cooperative eye hypothesis (Tomasello *et al.*, 2007). In other words, we explored whether available gaze information was reduced or non-existent in dark sclera eyes as they acted as gaze camouflage from conspecifics (Kobayashi & Kohshima, 2001); **2)** whether the use of the polarity reversal technique (the "Bogart illusion") highlighted any existing contrast differences between variable sclera colorations, e.g., can dark sclera eyes also provoke a "Bogart illusion"?; and **3)** whether there were differences in the degree of the "Bogart illusion" experienced by human observers that viewed gaze stimuli with human white sclera versus ape face stimuli with light sclera.

The stimulus categories could be broken down and/or compared from three perspectives in relationship to the cooperative eye hypothesis to better understand not only the potential contrast differences in the stimuli but also any species differences. These viewpoints were considered in light of participant reaction times and response accuracy measurements.

Dark sclera ape eyes: If information is available in dark sclera stimuli, then the participants are expected to respond accurately when making gaze direction judgments when viewing positive dark sclera ape eyes. If participants perceive a gaze reversal in dark sclera ape eyes, i.e., report a perception of gaze change on contrast inversion of the stimulus, then the cooperative eye hypothesis as it currently stands is not supported because the degree of available contrast observed in standard dark sclera ape eyes may be enough to transmit gaze information to at least a human observer.

Light sclera ape eyes vs. dark sclera ape eyes: If light sclera offers gaze direction benefits to an observer, then the participants are expected to have faster reaction times and more accurate responses for positive light sclera stimuli than for positive dark sclera stimuli. If the participants report a perceived gaze reversal in eyes with natural light sclera but not in those with dark sclera, then the cooperative eye hypothesis is supported in the sense that light sclera provides information concerning gaze direction that dark sclera does not.

Ape eyes vs. human eyes: Participants are expected to have the fastest reaction times and most accurate responses when viewing human stimuli in positive polarity. If the participants do not perceive a gaze reversal in *any* of the ape eye stimuli, then this supports the cooperative eye hypothesis in that great ape eyes do not convey accurate gaze information. In this case, it is not only the light sclera but also the configuration of the human eye that is necessary for enhanced gaze information. This would also lend support to the Tomasello *et al.* (2007) finding that apes rely more on head and body orientation over the eyes to determine the gaze direction of conspecifics.

The stimuli database consisted of the "positive" and "negative" groups and contained a total of 160 stimuli (Table 10). Each of the five species had a total of 32 positive and negative stimuli examples and all species combined had grand totals of 70 left gazing, 20 center gazing, and 70 right gazing stimuli.

The ape stimuli consisted of both dark sclera apes, and where suitable examples were observed, natural examples of apes possessing a light sclera (humans, gorillas, and orangutans). Dark sclera ape stimuli accounted for 66.2% of the total trials in the experiment with light sclera ape stimuli comprising 13.7% and human stimuli 20.1%.

Species	Stimuli count	Light sclera count
Bonobo	32	-
Chimpanzee	32	-
Gorilla	32	12
Human	32	32
Orangutan	32	10

Table 10 – The total number of stimuli per species, per trial presented to each participant (160 total stimuli per participant trial). Stimuli with light sclera accounted for 34.0% of the viewed stimuli.

3. Procedure

All stimuli were input into a custom computer program, "Gape", developed specifically for this task. "Gape" collected information on age, gender and a predetermined ID number at the start of the experiment. The gaze direction of the stimulus was evaluated from the perspective of the observer, i.e., a left-gazing stimulus was one that was directed to the left of the participant. The three response keys on the keyboard were labeled for participants: the **"A"** key an L (for left gaze), the **"spacebar"** a C (for center gaze), and the **"L"** key an R (for right gaze). These response keys were chosen because of their left, center, and right locations on the keyboard and this relationship to the corresponding left,

center, and right directions of the stimulus gaze presented on-screen. The participants were then provided with a practice trial of 6 photographs in positive and negative polarities to acclimate them to the experimental procedure.

The stimuli were presented to the participants on a mid-point grey background on an 18" computer monitor and each participant sat approximately 60 cm away from the monitor. All stimuli were presented in a random order of polarities, species, and gaze directions, which were determined by the Gape program. The participants were asked to look at a fixation cross in the center of the screen during the inter-trial intervals (1000 ms) and then respond with the appropriate key press when the stimulus appeared. All stimuli were presented at a 55% width on-screen until an approved response was made or for a maximum of 3000 ms at which time the stimulus timed out. The program automatically granted a break when the participants reached the halfway point in the trials (80 stimuli).

4. Response measurements

Participant input for each stimulus was gauged for both reaction time (ms) and accuracy (correct response or an error) to further investigate how quickly and accurately the participants were able to judge the gaze directions of the varying stimuli. Any response with a RT > 3000 ms was excluded from the analysis because the Gape program "timed-out" and coded the trial with an automatic error. An additional trial with a RT = 78 ms was also eliminated because of participant response aberration (excluded data accounted for 1.1% of all trials). The accuracy in gaze direction judgments was evaluated based on a labeling system for each individual stimulus. Each stimulus was identified by a two letter prefix, an underscore, and a species label (Fig. 8). The first letter of the prefix was

a reference to polarity: either **p** (positive) or **n** (negative), and the second letter was a reference to gaze direction: **l** (left), **c** (center), or **r** (right). The species were then simply labeled by the first letter: b (bonobo), c (chimpanzee), etc. For example, a stimulus with the label pr_b1.jpg stood for positive right gazing bonobo stimulus #1. The gaze direction label for the positive stimulus was retained when the stimulus was inverted to negative polarity thus making the equivalent of the above example: nr_b1.jpg. Errors were then recorded as a deviation from the predetermined direction of the positive polarity stimulus. For example, if a participant viewed nr_b1.jpg and input an "L" as the perceived gaze direction, Gape scored this as an error.

These positive and corresponding negative stimulus examples are unavailable due to copyright restrictions.

Fig. 8 – Examples of the positive and corresponding negative stimulus viewed by the participants. Note: the stimulus label was not visible to the participants but is included in the above figure for clarity.

Results

Participants were highly accurate at judging gaze direction when presented with positive human eyes (*accuracy* = 95.8%). They also demonstrated an overall adeptness at judging the gaze direction of positive ape eyes (*accuracy* = 67.1%; light and dark sclera apes).

1. Positive polarity: dark and light sclera stimuli

The overall comparison of dark sclera stimuli (bonobos, chimpanzees, gorillas, and orangutans) and light sclera stimuli (gorillas, humans, and orangutans) showed that participants committed significantly fewer errors when judging gaze direction in light sclera stimuli in comparison to dark sclera stimuli (*light sclera error* = 3.6%; *dark sclera error* = 38.6%; $\chi^2_{(1)} = 422.8$, $p < .001$) [Table 11]. Additionally, the participants were significantly faster when responding to light sclera stimuli than dark sclera stimuli (*Wilcoxon-signed rank test*: $z = -5.4$, $p < .001$) [Table 11, Fig. 10 top]. Although more errors were made when dark sclera stimuli were viewed, participant responses were correct significantly more often than incorrect ($\chi^2_{(1)} = 108.8$, $p < .001$).

Stimulus type	(+) Polarity error	(+) *n*	(-) Polarity error	(-) *n*	(+) Mean RT (ms)	(-) Mean RT (ms)
Dark sclera	*38.6%	803	*56.5%	1175	*916.68 ± 8.2	960.56 ± 9.3
Light sclera	3.6%	36	28.7%	286	717.24 ± 8.5	945.59 ± 13.1

Table 11 – The error (%) and reaction time values (± SEM) for dark and light sclera stimuli. Significant relationships (*) were observed between dark and light sclera values for positive error, negative error, and positive reaction time (human and light sclera apes were both incorporated in the light sclera category).

Participant accuracy was high and RT was low when positive human eyes were viewed (701.3 ms, 4.2%) [Table 12]. A significant difference between direct and averted gaze RTs was observed for human stimuli with faster RTs for averted gazes (669.2 ms) than direct gazes (926.1) [*Wilcoxon-signed ranks test*: $z = 5.4$, $p < .001$; Table 13]. The overall error was lower when participants viewed averted human gazes (0.5%) than direct gazes (29.5%). When participants erroneously judged gaze direction in direct human eyes, 95.6% of these errors occurred when one particular stimulus was viewed that was labeled as center gazing but was perceived as gazing to the right (Fig. 9). Because of the

high levels of error pertaining to this particular stimulus, it was removed from the subsequent analyses.

This aberrant stimulus example is unavailable due to copyright restrictions.

Fig. 9 – The human stimulus that resulted in 22 of 26 total positive errors. All participants input that the stimulus was gazing to the right, which may have resulted from the slight incongruence between the direction of eye gaze and the head orientation.

A Friedman's test was used to test for RT differences between the light sclera species, and it was observed that the RTs differed significantly across the three species ($\chi^2_{(2)}$ = 22.2, $p < .001$). Post-hoc Wilcoxon-signed ranks tests with a Bonferroni adjustment indicated that RTs were comparable for orangutans (689.34 ms) and humans (679.07 ms; z = -.6, p = .530), and gorilla RT (779.02 ms) was significantly slower than either orangutans (z = -3.5, p = .001) or humans (z = -4.4, $p < .001$). In addition to be being adept at judging gaze direction in human stimuli (99.3% accuracy, n = 4 errors), the participants were also adept at distinguishing gaze direction in light sclera orangutan (99.4% accuracy, n = 1 error) and gorilla eyes (96.1% accuracy, n = 9 errors).

Stimulus type	(+) Polarity error	(+) *n*	(-) Polarity error	(-) *n*	(+) Mean RT (ms)	(-) Mean RT (ms)
Dark Sclera Apes – *Overall*	***38.6%**	**803**	**56.5%**	**1175**	***922.1 ± 30.0**	**969.4 ± 41.2**
Bonobo	*39.0%	241	58.2%	359	*921.4 ± 33.1	966.9 ± 41.3
Chimpanzee	*36.0%	223	50.8%	312	*897.6 ± 38.6	958.7 ± 44.0
Gorilla	42.2%	162	47.5%	183	*946.4 ± 43.7	1008.0 ± 45.9
Orangutan	*38.5%	177	69.3%	321	935.4 ± 37.2	954.6 ± 44.1
Light Sclera Apes – *Overall*	***2.6%**	**10**	**37.3%**	**142**	***743.7 ± 26.0**	**986.4 ± 51.0**
Gorilla	*3.9%	9	40.3%	92	*779.0 ± 28.7	1016.7 ± 51.1
Orangutan	*0.6%	1	32.7%	50	*689.3 ± 30.3	941.1 ± 57.8
Human	***0.7%**	**4**	**21.7%**	**125**	***679.1 ± 23.6**	**930.3** ± 40.6

(*) Indicates a significant relationship between the positive and negative values for that particular stimulus type.

Table 12 – The table illustrates the overall participant error (%) and mean RTs (± SEM) for the three stimulus categories and individual species types belonging to each category. The individual species error percentages are illustrative of the amount of participant error when a stimulus of that species was viewed (e.g., participants made inaccurate gaze judgments in 39.0% of trials when viewing positive bonobo stimuli; when the polarity was inverted, participants made errors in 58.2% of trials). Error increased significantly for all species when the polarity of the stimulus was negative except for dark sclera gorillas. Significant differences were also observed for all species (except dark sclera gorillas) between positive and negative mean RTs.

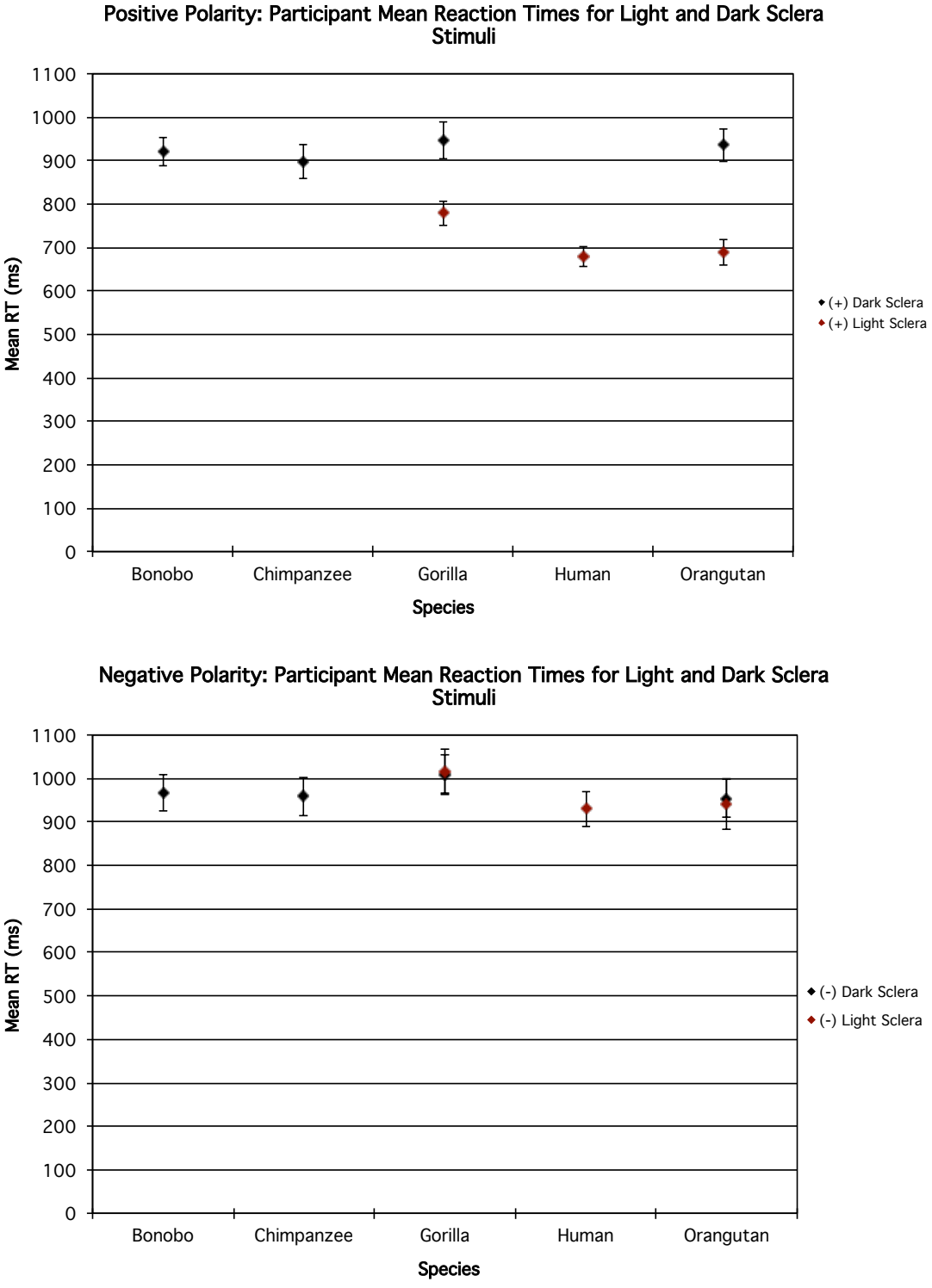


Fig. 10 – Species-specific reaction times when the participants viewed positive (**top**) and negative stimuli (**bottom**). The participants responded faster when viewing positive stimuli and when the stimulus contained a light sclera.

Stimulus type and gaze direction	(+) Polarity error	(+) n	(-) Polarity error	(-) n
Dark Sclera Apes				
Direct	*26.4%	81	*23.9%	74
Averted	40.7%	722	62.2%	1101
Light Sclera Apes				
Direct	-	-	-	-
Averted	2.6%	10	37.3%	142
Humans				
Direct	2.6%	1	*10.5%	4
Averted	0.5%	3	22.4%	121

Table 13 – The positive and negative error proportions for stimuli categorized by gaze direction (direct or averted) and stimulus group. Significant relationships (*) were observed between direct and averted gazes for the positive and negative dark sclera apes and negative human stimulus groups.

(+) Stimulus type	Direct gazes (ms)	Averted gazes (ms)
Dark Sclera Apes		
(Overall)	**903.9 ± 34.7**	**924.9 ± 37.1**
Bonobo	*841.7 ± 45.9	931.8 ± 34.3
Chimpanzee	934.0 ± 51.3	892.1 ± 39.0
Gorilla	919.9 ± 52.7	954.7 ± 44.3
Orangutan	912.6 ± 40.3	937.0 ± 40.4
Light Sclera Apes		
(Overall)	**-**	**743.9 ± 26.0**
Gorilla	-	779.1 ± 28.7
Orangutan	-	691.6 ± 30.0
Humans	***817.4 ± 39.3**	**669.2 ± 23.1**

Table 14 – The mean participant reaction times (± SEM) categorized by stimulus type and gaze direction (direct or averted) for positive polarity. (*) Indicates a significant difference between the direct and averted RT values within a particular stimuli group.

The most participant error occurred overall when dark sclera apes were viewed, and the RT was significantly slower than ape stimuli with light sclera (*Wilcoxon-signed ranks test*: $z = -5.4$, $p < .001$) [Table 13]. Participants committed more errors when averted

gazes were viewed (Table 12), and of these errors, participants most frequently perceived the stimulus gaze as slightly deviated from the labeled gaze direction (i.e., averted gazes were perceived as center gazing in 91.2% of errors). A Wilcoxon-signed ranks test revealed a significant difference between direct and averted gaze RTs for dark sclera bonobos (z = -3.1, p = .002) and human stimuli (z = -4.6, p < .001) [Table 14]; however, no significant differences were observed for any other direct and averted species comparisons (*dark sclera chimpanzees*: z = -1.1, p = .26; *dark sclera gorillas*: z = -1.5, p = .14; and *dark sclera orangutans*: z = -.5, p = .61).

2. Negative polarity: dark and light sclera stimuli

Overall, participants responded more slowly to negative polarity gazes than positive polarity (*Wilcoxon-signed ranks test*: z = -5.4, p < .001) [Fig. 10 above], and with the exception of human gazes, tended to respond more quickly when presented with direct gazes than averted gazes (*Wilcoxon-signed ranks test*: z = -2.8, p = .006). This tendency was significant for dark sclera apes as an entire group (*Wilcoxon-signed ranks test*: z = -2.9, p = .004) and when viewing dark sclera bonobos (*Wilcoxon-signed ranks test*: z = -2.8, p = .005) and chimpanzees (*Wilcoxon-signed ranks test*: z = -2.2, p = .031) [Table 15]. Response error was significantly higher for negative polarity than positive polarity for all three stimulus categories (*dark sclera apes:* $\chi^2_{(1)} = 70.0$, p < .001; *light sclera apes*: $\chi^2_{(1)} = 114.6$, χ^2 .001; *human*: $\chi^2_{(1)} = 81.9$, p < .001) [Fig. 11]. Participants committed the most amount of overall errors when viewing negative dark sclera apes (56.5%) and were also significantly more frequent in making an error than a correct response for this stimuli group ($\chi^2_{(1)} = 35.3$, p < .001).

(-) Stimulus type	Direct gazes (ms)	Averted gazes (ms)
Dark Sclera Apes		
(Overall)	***913.9 ± 38.6**	**979.74 ± 42.2**
Bonobo	*852.6 ± 38.6	982.6 ± 44.1
Chimpanzee	*902.9 ± 60.2	966.0 ± 42.7
Gorilla	958.4 ± 47.9	1020.4 ± 48.9
Orangutan	928.4 ± 45.7	958.6 ± 45.9
Light Sclera Apes		
(Overall)	-	**964.56 ± 42.2**
Gorilla	-	1016.7 ± 51.1
Orangutan	-	941.1 ± 57.8
Humans	**877.8 ± 53.3**	**922.5 ± 41.5**

Table 15 – The mean participant reaction times (± SEM) categorized by stimulus type and gaze direction (direct or averted) for negative polarity. (*) Indicates a significant difference ($p < 0.05$) between the direct and averted RT values within a particular stimulus group.

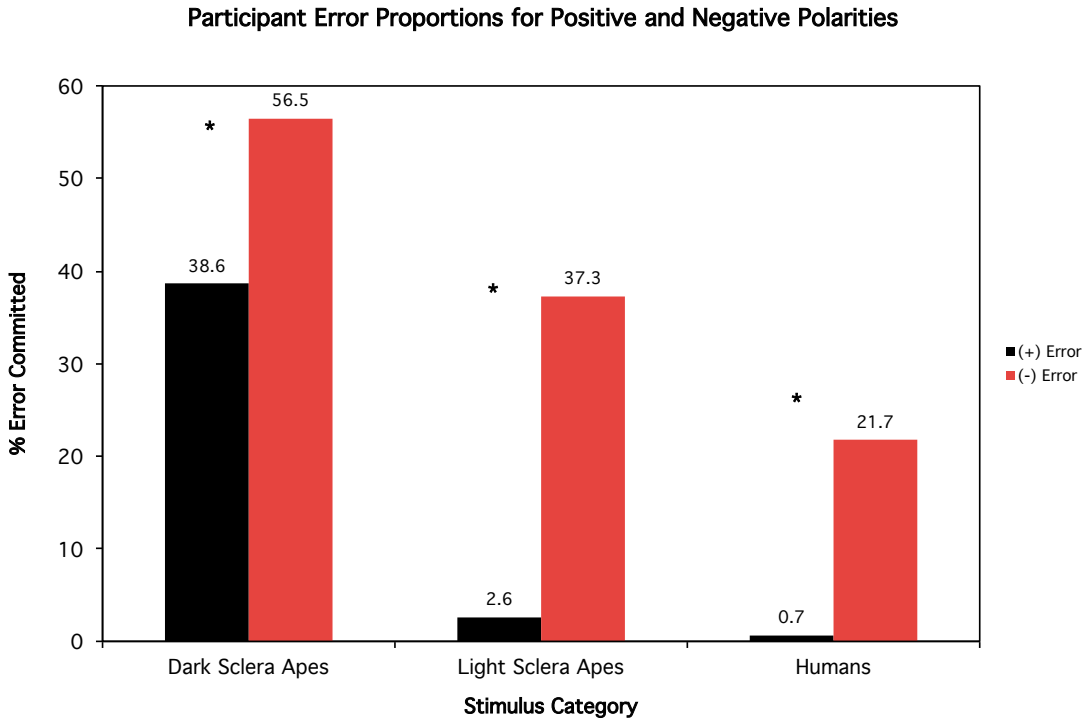


Fig. 11 – This graph reports the participant response error proportions for positive and negative polarities for each of the three stimulus categories. Significant differences (*) were observed for all three stimulus categories between positive and negative polarity error.

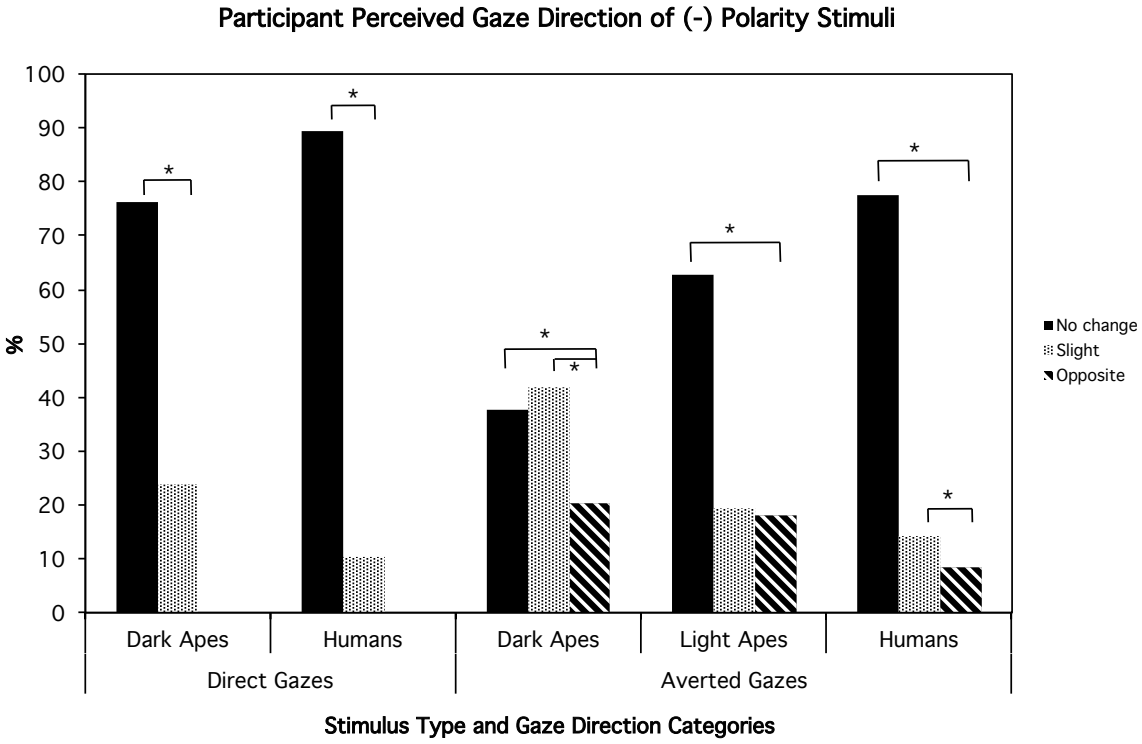


Fig. 12 – The reported perceived gaze when participants viewed negative polarity gazes. Significant relationships were observed for all three stimulus groups for the overall averted gaze response distributions; responses to dark sclera ape stimuli were more frequently reported as center-oriented, whereas participants more frequently reported no gaze reversal for light sclera apes and humans. Additional gaze reversal relationships were significant for the perception of a center-oriented reversal when viewing dark sclera apes and humans. Participants reported nearly equal amounts of a center-oriented and complete reversal when viewing light sclera apes.

Error increased for both light sclera and humans from positive, low baseline values (*light sclera apes* = 2.6%, n = 10; *humans* = 0.7%, n = 4) to negative, higher amounts (*light sclera apes* = 37.3%, n = 142; *humans* = 21.7%, n = 125). Overall, participants did not report the perception of a gaze reversal when viewing either light sclera apes or humans, and this result was significant for both light sclera apes ($\chi^2_{(2)} = 148.2$, $p < .001$) and human stimuli ($\chi^2_{(2)} = 476.9$, $p < .001$). When participants perceived a gaze reversal for light sclera apes (37.3% of light sclera error) it was perceived as center-oriented or completely reversed nearly equally (*center* = 51.4%, n = 73; *opposite* = 48.6%, n = 69;

$\chi^2_{(2)} = .113$, $p = .737$). Surprisingly, the perceived reversal for human gazes was not as evenly matched as observed for light sclera apes, and instead, participants reported a center-oriented reversal more frequently than a complete reversal ($\chi^2_{(1)} = 7.942$, $p < .001$) [see Fig. 12].

Discussion

This contrast reversal study using naturally occurring examples of dark and light sclera great apes and humans was an exploration of: 1) whether non-human great ape eyes with dark sclera lack gaze information; 2) whether polarity reversal presents contrast differences between variable sclera colorations; and 3) whether human observers experienced the Bogart illusion with ape and human faces that contained light sclera.

1. Gaze direction judgments: positive stimuli

As expected, this study reported that participants overall performed accurately and quickly when viewing human gazes in positive polarity. Unexpectedly, participants also tended to perform quickly and accurately when positive light sclera ape gazes were viewed, which generated RTs and error results that were comparable to those for human gaze responses. In comparison to light sclera counterparts, participants demonstrated significantly slower and less accurate responses when dark sclera ape gazes were viewed. Although the responses were less accurate, participants were still able to significantly discern gaze direction correctly for this stimulus group ≥ 61% of the time.

1.1. *Direct and averted gazes*

The isolation of stimulus gaze direction for the three stimulus groups allowed for the

comparison between direct gazing dark sclera apes and humans (but not light sclera apes) and averted gaze responses for all three groups. Participants were observed to respond significantly slower to direct gazes than averted gazes; however, participants were accurate when presented with either type. The slower direct gazing human RT was comparable to the species RTs for dark sclera apes, which indicated that participants were judging gaze directions in direct human gazes and direct dark sclera ape gazes for similar amounts of time. A comparison of averted gazing light sclera ape and human responses revealed that participants were nearly perfect in gaze direction judgments and had comparable RTs for orangutans and humans. Of the light sclera species comparisons, participants were slightly slower and less accurate in the gaze direction judgments of gorillas but remained adept at an accurate evaluation of gaze direction.

Contrary to gazes with a lightened sclera, participants responded less accurately and more slowly to averted dark sclera gazes. Clearly, the more uniform color distribution in the dark sclera ape face made the determination of gaze direction more difficult; however, the participants appeared to cope with this fairly well to generate accuracy in gaze direction detection. When errors were committed, it was rare that participants grossly misjudged the gaze direction and were actually more likely to report the gaze as being center-oriented. The overall lower response accuracy for this stimulus group may have been the result of a few contributing factors: 1) non-human great ape eyes are a stimulus that humans are not accustomed to seeing on a daily basis. This stimulus novelty in addition to the small amount of available color differentiation in the dark-dark contrast between the iris, sclera, and skin of this stimuli group may have presented participants

with particular difficulty; 2) it is possible that the form of the stimulus – which attempted to control for any extraneous facial cues – influenced participant efficiency at gauging gaze direction. It is conceivable that gaze direction accuracy would increase with the inclusion of the nose, the brow ridges, or additional facial cues in the stimulus to guide judgments of gaze direction; and 3) the inclusion of the "timed" aspect of this study may have potentially negatively influenced gaze direction accuracy, as participants were told to respond to each stimulus as quickly as possible. If the participants were faced with a more difficult stimulus, such as one with uniform dark colorations, then having additional time to produce a response may generate a more accurate response.

In general, the dark sclera results indicate that in the absence of a classic light-and-dark contrast, sufficient information is available in the eye region for a human observer to make an accurate, or near accurate estimation of dark sclera ape gaze direction. However, participants exhibited comparably quick and accurate responses for both light sclera ape and human gazes, although the eyes of naturally existing light sclera apes are morphologically different from humans. This highlights that the lightened sclera characteristic that was common to both stimulus groups, generated similar effects of accurate gaze direction detection by the human participants, regardless of whether the surrounding face was non-human ape or human.

The discussion of gorilla and human eye morphologies in Chapter 2 highlighted that the human eye remains unique from the other great apes in its horizontal elongation (an increased width/height ratio) but not in its singularity of sclera coloration. As this study

shows, the addition of a lightened sclera to ape eyes appears to contribute favorably to more accurate and rapid on-looker RTs, especially in the occurrence of averted gazes. The comparability between species with a light sclera indicates that an eye elongation may not necessarily be important for gaze direction detection in averted gazes and that the presence of a light sclera suitably emphasizes gaze direction. The critical evolutionary change in the human eye may therefore have been the horizontal eye elongation as a mechanism to maximize the effect of a light sclera, particularly in the case of a direct gaze. This however needs further verification with examples of direct gazing light sclera apes to draw an informative comparison with direct gazing humans.

2. Bogart illusion effects: negative stimuli

The overall participant error increased for all three stimuli groups when gazes were presented in negative polarity, thereby showing some evidence of a Bogart effect. In other words, the error generated by the polarity inversion indicated that participants perceived gaze direction changes in the three negative stimuli groups.

2.1. *Direct and averted gazes*

The comparison of averted gazes revealed that participants significantly perceived gaze changes in all three stimuli groups, although the effect for light sclera averted gazes was not as large as anticipated. Averted human gazes also appeared to generate more gaze change than direct human gazes. Participants demonstrated lower amounts of perceived gaze direction changes in light sclera orangutans and human gazes with slightly more error when viewing light sclera gorillas. Species coloration differences may have contributed to these species differences, and the stronger contrast differences in the eye

regions of gorillas may have created a more pronounced Bogart effect. Conversely, the paler skin and red-orange color of orangutans may have produced a lighter and less heavily contrasted negative stimulus and thus decreased the perceived Bogart effect. Overall, there was some evidence for the perception of complete gaze reversals in both human and light sclera ape gazes; however, the complete reversal effect was more pronounced in averted light sclera apes than in averted human gazes.

Changes in gaze direction were reported more frequently for averted dark sclera gazes than light sclera averted gazes, and these dark sclera averted gazes were significantly perceived as being center-oriented; however, some gazes were reported as being directed in the complete opposite direction, which indicated that an aspect within the stimulus might have been sufficient enough to cause a complete Bogart effect. This was an unexpected result because dark sclera eyes lack the classic contrast cues central to generating the Bogart illusion, and it was therefore anticipated that a polarity inversion would not cause any perceived gaze changes. However, because our results indicated otherwise, the perception of a gaze change may actually be an indication that there are other attributes, besides eye contrasts, within the morphology of the face that are disrupted by a polarity inversion.

Ultimately, the results for dark sclera apes lend support to the idea that information appears to be effectively garnered from all-dark eyes and additional cues may work in combination to further enhance gaze direction. Traditionally, apes have been suggested to rely on head and body orientation to determine gaze direction, and this reliance on

gross gaze cues has linked all-dark ape eyes to a supposed lack of gaze direction information. However, this study eliminated both the head and body from the stimuli, which suggests that at least for human observers, the eye region of apes may contain directionality information in other morphological features that work outside of dark-and-light contrasts of the eyeball. Features such as the eyebrows, nose, and periocular region (e.g., eyelids, skin around the eyes, etc.) may contain cues of gaze direction, at least to a human observer.

The exact components of the dark sclera stimuli that were conducive to the generation of a Bogart illusion have yet to be determined. One interesting consideration is the effect of any artificial and/or ambient light within the stimulus. The flash of a photographer's camera can cause artificial bright spots and the ambient light in naturalistic settings can cause illumination in an otherwise dense jungle setting. For positive dark sclera ape eyes, these reflections of environmental light off the eye tissues may have acted as gaze enhancers by creating an artificial dark/light contrast. These glares, being bright in positive polarity, would have been dark when the polarity was inverted. Therefore, in some cases, a reflection of ambient light off of the sclera of the photograph subject may have been amplified to resemble something like a false iris and contributed to the perception of a gaze reversal in the negative stimuli. The present stimuli were not manipulated to control for any artificial additions; however, these manipulations were considered for the follow-up study (Experiment 2).

3. Comparison to the original Bogart study: human stimuli

Both this study and Sinha's earlier results (Sinha, 2000) were comparable for positive

polarity human gazes (*Sinha* = 100% accuracy, *this study* = 99.3% accuracy). However, contrary to what Sinha had reported, the present study failed to illustrate such a large Bogart effect for negative human stimuli. Sinha's earlier report of a 60-80% perceived gaze reversal was much higher than the 21.7% reversal observed here. Even the results for light sclera apes failed to generate such a high degree of perceived gaze reversal (37.3%). The disparity between the results of this study and the original may lie in study design. In the original, the participants strictly viewed 8 human full-face stimuli whereas this study used 32 human eye-region stimuli, interspersed randomly with numerous ape eye-region stimuli. The full-face stimuli of the original study potentially contained more gaze direction cues and more areas of light/dark contrast that could have been influenced by polarity reversal, which possibly reinforced the gaze reversal effect. The original study also had only two response options (left and right) and the present study introduced a third "center" option. This was implemented in an attempt to determine whether a polarity change actually signified the perception of a complete gaze reversal or if there were other perception possibilities. The present study observed that in fact, most participants perceived a center-oriented gaze change rather than experiencing a full-reversal effect. In general, the results of the present study reflect the perception of the Bogart illusion in the sense that a perceived gaze change was only evident to participants to some degree. However, the increased number of stimuli, the removal of other face and head related cues, and the introduction of the third response option may have been responsible for its low presence in comparison to the original study. Taking these variables into consideration, further modifications were made to the methodology to conduct Experiment 2 in an attempt to address some of the above issues and account for

such a low Bogart effect.

4. Summary

Overall, this study observed that when present, light sclera is a useful characteristic for determining gaze direction in others both quickly and accurately. This was demonstrated even in the absence of further morphological changes (especially the elongation of the human eye) by the lack of significant differences between natural human and light sclera ape eyes. This light sclera result supports the cooperative eye hypothesis (Tomasello *et al*., 2007) in the sense that the evolution of a light sclera adaptation would have been beneficial for joint attentional social interactions that relied heavily on judgments of eye gaze direction. Yet, this study also observed that humans are proficient at gaze direction judgments of unconventional dark sclera ape eyes. This indicates that human gaze determination capabilities are excellent and can be flexibly employed, and do not rely on a single gaze cue, such as a polarity contrast. This also indicates that great ape eyes contain gaze information at a high enough level that a human observer is capable of collecting and using that information to make an accurate judgment. Such results might challenge some of the current assumptions about the cues used by the great apes to determine attention in other individuals. While head and body orientations have been demonstrated to be used by apes, the extent to which great apes could use the gaze direction information that we have shown exists in the eyes of conspecifics is still a relatively open question.

II. Experiment 2

Summary

The aim of the second experiment was to further probe the relatively low magnitude of the Bogart effects observed in Experiment 1, which contrast with the original study (Sinha, 2000). Modifications to both the stimuli and the response options were made to address some of the possibilities discussed in Experiment 1 as the potential causes of the low Bogart effect that was observed for human stimuli. These changes included: 1) the collection and modification of new stimuli to control for artificial or ambient glares on the eyeball of the subject; 2) the addition of the full-face Bogart stimuli from the Sinha original 2000 experiment; and 3) the elimination of "center" as both a stimulus gaze and a response option. These changes were made based on the results observed in Experiment 1. Again, as secondary objectives, we investigated: 1) whether dark sclera eyes lack useful gaze information; 2) if contrast differences exist between light and dark sclera coloration types and if so, what the prevalence of these differences was; and 3) if the light sclera of the human eye differs from the light sclera ape eye in terms of provoking the Bogart illusion.

Methods

1. Subjects

This experiment used 28 consenting University of St Andrews students with ages ranging from 18 to 21 (female $n = 21$, male $n = 7$); all had normal or corrected-to-normal vision. Subjects were recruited using the University of St. Andrews SONA Research Participation System. The participants were provided with an information sheet outlining

their role in the study after which they were given the opportunity to ask questions and sign a form consenting to their participation. The experiment was conducted in the Psychology building at the University of St. Andrews, Scotland.

2. Stimuli

The stimuli from Experiment 1 were re-evaluated to determine whether there was any ambiguity in the projected gaze direction of the eyes, i.e., cues that could potentially be regarded as "center-oriented" were excluded. Experiment 1 center gazing individuals were excluded from this study, in addition to examples that had potentially confounding head orientations and eye gaze cues (incongruency) and stimuli that were lower in quality (showed some pixilation or were further away from the camera) were replaced with examples of closer, high-quality photographs. In the majority of instances, the stimuli of Experiment 2 included new examples of each species. Again, black-and-white photographs were collected from online resources (via Google images) for each of the five species (bonobo, chimpanzee, gorilla, human, and orangutan), and additionally for this study, the eight full-face stimuli used in the original Bogart experiment were included (Sinha, 2000). The photographs were again cropped using the MacOSX Preview application (v. 5.0.3) to isolate the eye region (except for the subset of Bogart faces). The eye region was established as it was in Experiment 1: based on a set of rough anatomical boundaries that excluded the nasal region below, the forehead above and bordered laterally on the outer edge of the zygomatic arches. This again resulted in a variation of stimuli sizes based on species and individualistic anatomical variability; therefore, each stimulus was presented onscreen at a set width of 57.0%, which provided an overall uniformity in viewing size to the participants. Modifications to some of the

stimuli (Fig. 13) to remove any ambient glare on the eyeball of the individual were made using the clone tool in Gimp (a GNU Image Manipulation Program, v. 2.6.11) to provide a more uniform coloration to the affected part. Modifications did not need to be made to the majority of the stimuli, and the stimulus was only included in the dataset if the necessary touch-ups were minor.

This illustration demonstrating a modification to a gorilla stimulus is unavailable due to copyright restrictions.

Fig. 13 – An illustration of the modification made to a gorilla stimulus to remove the ambient glare from the right eye.

These original Bogart illusion stimulus examples are unavailable due to copyright restrictions.

Fig. 14 – The original positive and negative stimuli taken from Sinha's (2000) study and used, unmodified, as a subset of stimuli for the current study.

The stimuli database consisted of a positive polarity group containing light and dark sclera eyes that were gazing to either the left or right. The gaze direction of the stimulus was evaluated from the perspective of the observer, i.e., a right gazing stimulus was one with a gaze that was directed to the right of the participant. Again, the stimuli were flipped on the vertical axis to create a mirror image, yielding two positive images. All stimuli were then duplicated, and the polarity was negated to create a second negative polarity group. The total stimuli dataset contained 220 stimuli (positive and negative; bonobo, chimpanzee, gorilla, orangutan, human, and Bogart examples) and 176 of these stimuli had light sclera.

Stimulus species	No. of stimuli	No. of light sclera
Bonobo	20	12
Chimpanzee	16	-
Gorilla	76	64
Human	52	52
Orangutan	40	32
Bogart face	16	16

Table 16 - The total number of stimuli that each participant observed (220 total, 176 with white sclera). The only species without a white sclera representative was the chimpanzee.

3. Procedure

As was performed in Experiment 1, each individual stimulus was identified by a 2-letter prefix, an underscore, and a species label (see Experiment 1 for complete coding methodology). This study also introduced the full-face Bogart stimuli from the Sinha (2000) study, which were designated with "Bogart" as their species label. The custom developed "Gape" computer program collected age, gender, and a preset participant ID number from participants at the start of the task. The stimuli were presented on a mid-point grey background on an 18" computer monitor, and the participant sat approximately 60 centimeters away from the monitor (see Experiment 1 methodology for complete viewing procedure). The participants were instructed that the two response keys on the keyboard they were to use were the "**A**" key for a left gazing stimulus and the "**L**" key for a right gazing stimulus. The participants were then provided with a practice trial of five photographs in positive and negative polarities to acclimate them to the experimental procedure. Any response with a RT > 3000 ms (0.3% of cases) was excluded from the analyses because the Gape program "timed-out" and coded the trial with an automatic error.

4. Inter-observer reliability

A secondary coder labeled the gaze direction of 50% of the positive stimuli used in this experiment (all positive stimuli before they were flipped on the horizontal axis; $n = 106$) to assess inter-observer reliability. In gaze direction judgments, the primary (JM) and secondary coder (CF) agreed on 100% of the stimuli gaze directions (*Cohen's K* = 1).

Results

1. Positive gaze direction judgments: dark and light sclera apes

Participants were fast (612.4 ms) and nearly perfect at judging gaze direction in positive human eye stimuli (*error* = 0.5%, $n = 4$) [Table 17: I]. Participants were also accurate at judging the gaze direction of ape eyes overall when viewed in positive polarity (*error* = 2.6%, $n = 56$). A chi-squared test revealed that participants judged gaze direction significantly more accurately in light sclera stimuli (bonobos, gorillas, orangutans, and humans) than in those with dark sclera (bonobos, chimpanzees, gorillas, and orangutans) [*light sclera error* = 1.6%, $n = 35$; *dark sclera error* = 4.1%, $n = 25$; $\chi^2_{(1)} = 14.8$, $p < .001$; Table 17: II]. Mean RTs were also significantly quicker when responding to light sclera (636.3 ms) than dark sclera stimuli (720.4 ms) [*Wilcoxon-signed ranks test:* $z = -4.3$, $p < .001$; Fig. 15].

I.

Stimulus type	(+) Polarity error	(+) *n*	(-) Polarity error	(-) *n*	(+) Mean RT (ms)	(-) Mean RT (ms)
Dark Sclera Apes – *Overall*	***4.1%**	**25**	**8.0%**	**49**	***720.4 ± 24.5**	**797.9 ± 30.7**
Bonobo	9.8%	11	7.2%	8	782.8 ± 43.9	819.9 ± 44.3
Chimpanzee	4.5%	10	6.7%	15	*712.2 ± 26.2	787.9 ± 39.1
Gorilla	*0.6%	1	6.5%	11	*658.9 ± 23.0	775.2 ± 30.7
Orangutan	*2.7%	3	13.6%	15	769.4 ± 43.9	827.3 ± 50.3
Light Sclera Apes – *Overall*	***2.1%**	**31**	**21.9%**	**330**	***647.8 ± 17.4**	**781.2 ± 27.2**
Bonobo	*0.6%	1	21.4%	36	*646.4 ± 19.2	694.1 ± 22.0
Gorilla	*2.8%	25	22.8%	203	*645.8 ± 16.1	789.2 ± 27.6
Orangutan	*1.1%	5	20.5%	91	*652.0 ± 23.0	799.2 ± 33.6
Human	***0.5%**	**4**	**13.5%**	**98**	***612.4 ± 20.3**	**750.4 ± 30.2**
Bogart faces	***0.9%**	**2**	**7.6%**	**17**	***702.9 ± 21.7**	**935.4 ± 36.5**

(*) Significant difference observed between positive and negative values (for both polarity and RT).

II.

Stimulus type	(+) Polarity error	(+) *n*	(-) Polarity error	(-) *n*	(+) Mean RT (ms)	(-) Mean RT (ms)
Dark sclera	*4.1%	25	*8.0%	49	*720.4 ± 24.5	797.9 ± 30.7
Light sclera	1.6%	35	19.2%	428	*636.3 ± 17.8	771.3 ± 27.4

(*) Significant difference observed between dark and light values (humans incorporated in the light ape category).

Table 17 - Table I reports participant error (%) and mean RT (± SEM) for the three stimulus categories and individual species types. Individual species error percentages are illustrative of the amount of error committed when viewing that species (e.g., participants made inaccurate gaze judgments in 0.6% of trials when viewing positive dark sclera gorilla stimuli; when the polarity was inverted, participants made errors in 6.5% of trials). Table II reports participant error (%) and mean RT (± SEM) for overall dark and light sclera stimulus categories.

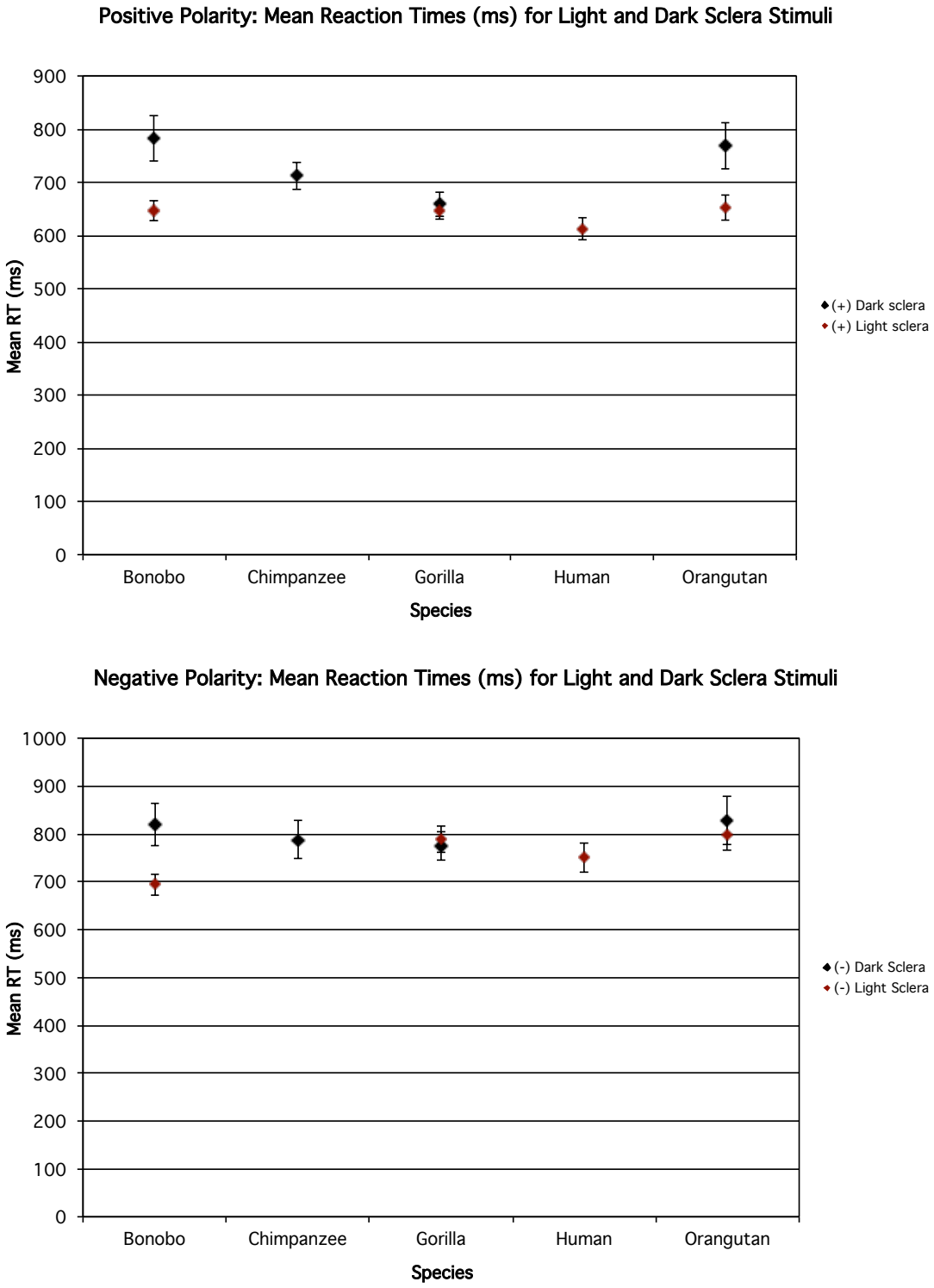


Fig. 15 – The participant mean reaction times when viewing positive (**top**) and negative stimuli (**bottom**). Participants responded faster when viewing positive stimuli and also when the stimulus contained a light sclera.

Participants judged positive light sclera ape gazes significantly more accurately than positive dark sclera ape gazes (*light sclera error* = 2.1%, n = 31; *dark sclera error* = 4.1%, n = 25; $\chi^2_{(1)} = 7.0$, $p = .008$; Table 17), and the mean RT for light sclera apes was also faster than when viewing dark sclera apes (*light sclera apes* = 647.8 ms; *dark sclera apes* = 720.4 ms; *Wilcoxon-signed ranks test*: $z = -4.1$, $p < .001$).

2. Bogart effects: negative dark and light stimuli

Participants committed greater amounts of error when negative stimuli were viewed, and this was significant for all three groups (*humans*: n = 98, 13.5%, $\chi^2_{(1)} = 93.4$, $p < .001$; *light sclera apes*: n = 330, 21.9%, $\chi^2_{(1)} = 282.7$, $p < .001$; *dark sclera apes*: n = 49, 8.0%, $\chi^2_{(1)} = 8.3$, $p = .003$) [Fig. 16, Table 17: I].

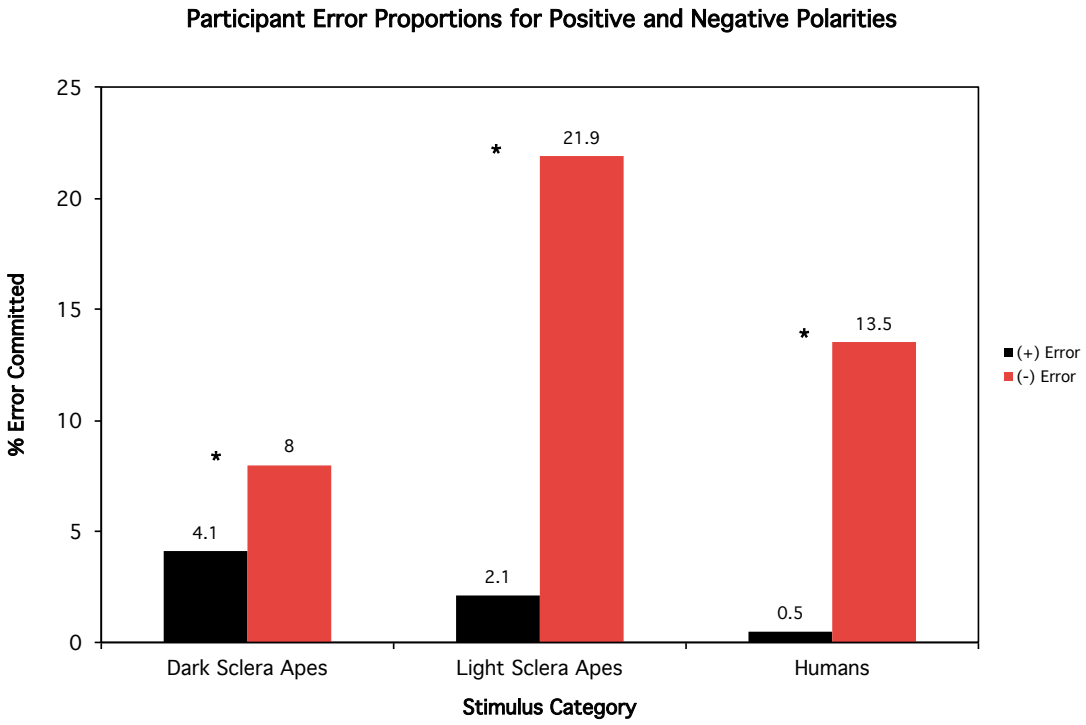


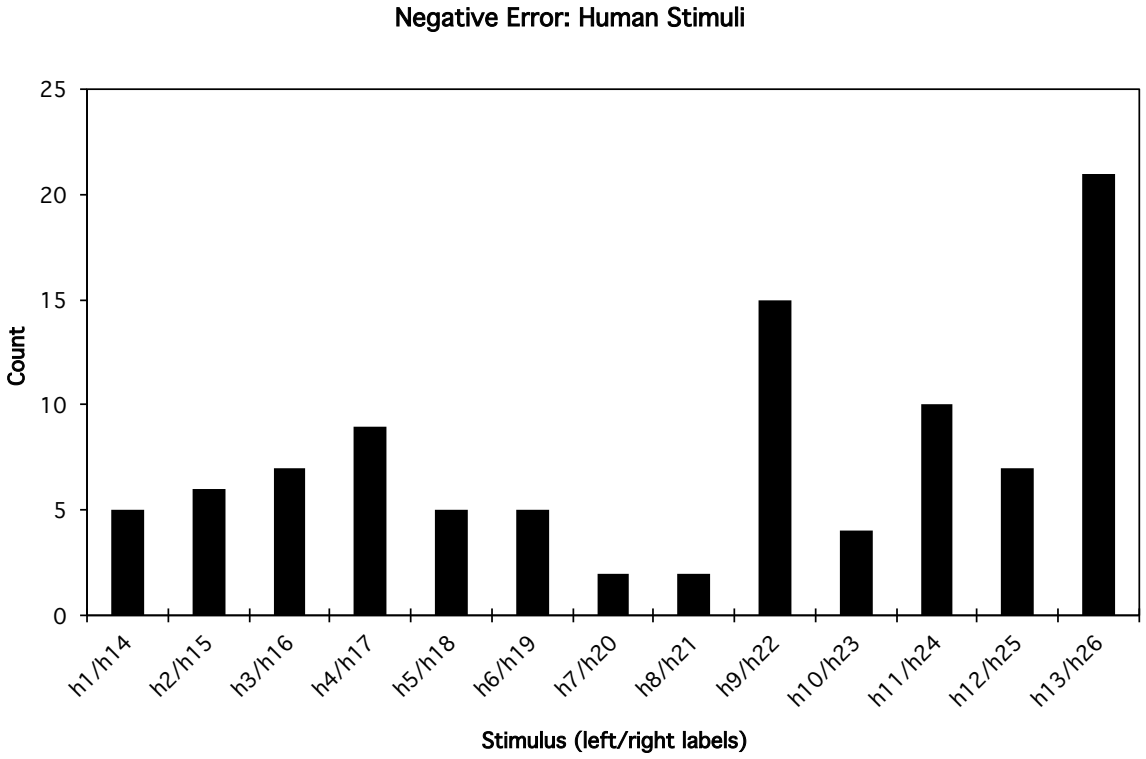
Fig. 16 – Participant error response proportions for positive and negative polarities of the three stimulus categories. Positive stimuli response errors were low in all three groups, and error increased significantly in all three groups when the polarity was inverted. Wilcoxon-signed ranks tests determined that positive RTs were also significantly faster

than negative RTs for all three groups (*humans*: $z = -4.5$, $p < .001$; *light sclera apes*: $z = -4.6$, $p < .001$; *dark sclera apes*: $z = -3.7$, $p < .001$) [Fig. 15, Table 17: I].

2.1. Stimuli contributions

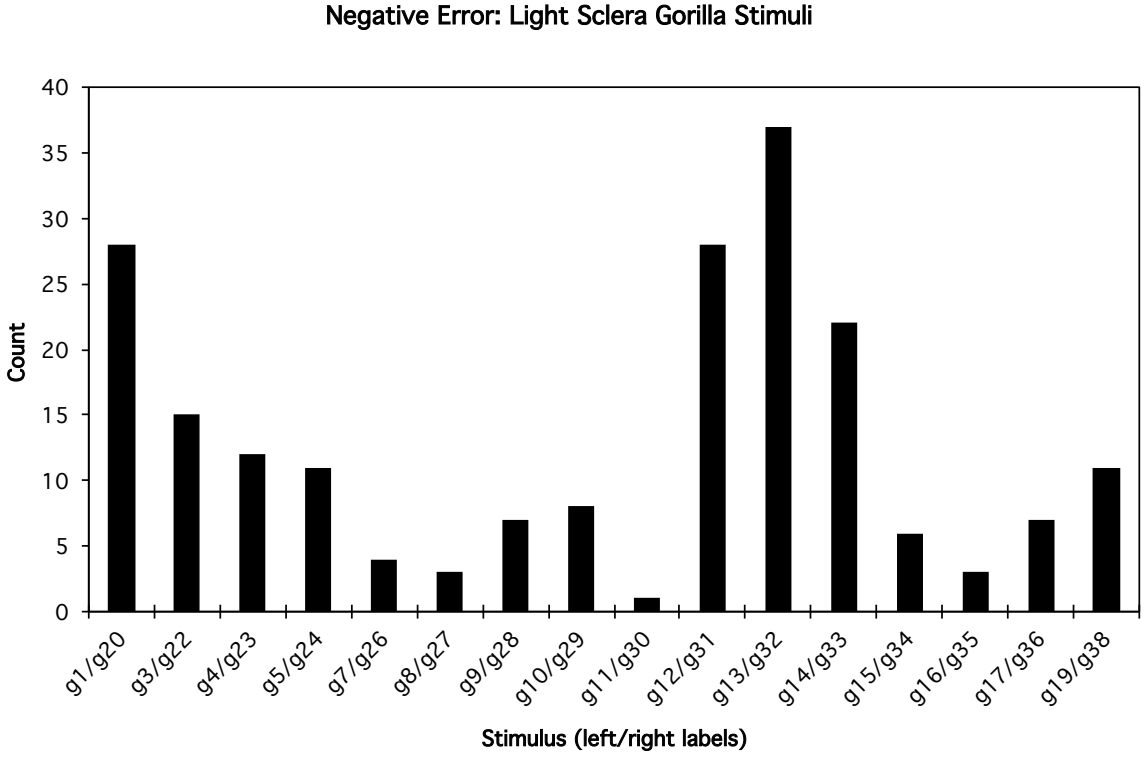
The individual negative errors were evaluated for the three stimulus groups to determine the species and stimulus contribution to gaze reversal perception (participant error). Participants perceived the lowest gaze reversal in negative dark sclera apes (8.0%, $n = 49$), and this was significantly lower than the perceived gaze reversal observed in either humans (13.5%, $n = 98$) or light sclera apes (21.9%, $n = 330$) [$\chi^2_{(2)} = 67.9$, $p < .001$]. When participants viewed human stimuli, they perceived gaze changes most frequently in stimulus h9/h22 (15 errors), h11/h24 (10 errors), and h13/h26 (21 errors) [Fig. 17].

An evaluation of light sclera ape error showed that participants perceived comparable amounts of gaze reversals in gorilla (22.8%, $n = 203$), bonobo (21.4%, $n = 36$), and orangutan stimuli (20.5%, $n = 91$) [$\chi^2_{(2)} = 0.9$, $p = .639$]. An individual stimulus evaluation determined that participants perceived gaze reversals most frequently when viewing gorilla stimulus g13/g32 (37 errors), orangutan stimulus o3/o13 (29 errors), and bonobo stimulus b3/b8 (27 errors) [Fig. 18, 19, & 20].



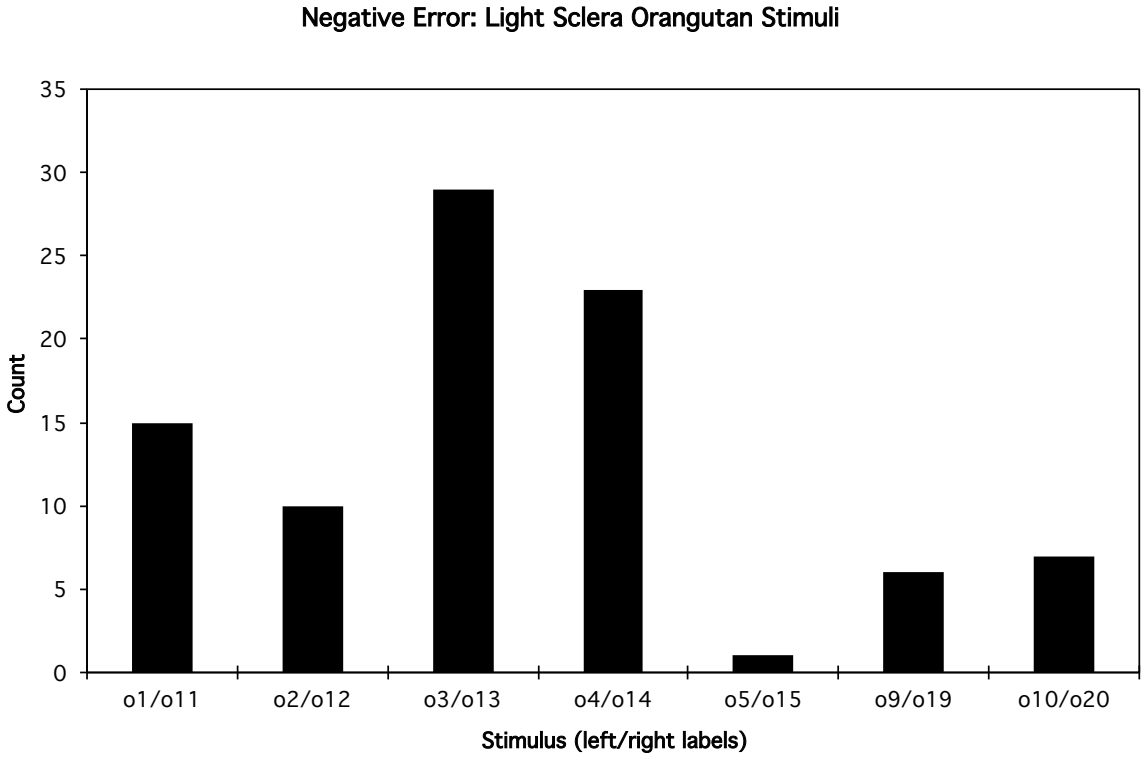
These negative human stimulus examples are unavailable due to copyright restrictions.

Fig. 17 – The top graph displays the distribution of participant error by the negative human stimulus viewed. Participants reported a perceived gaze reversal most frequently in the above three negative stimuli pictured.



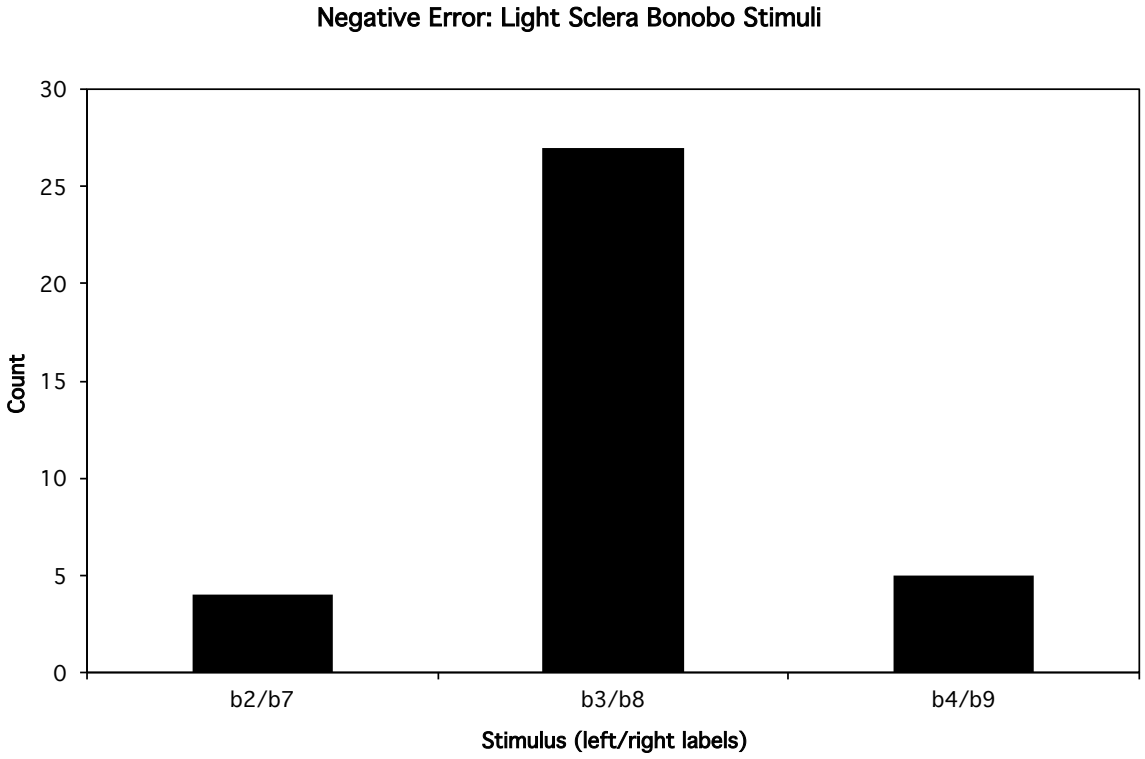
These negative gorilla stimulus examples are unavailable due to copyright restrictions.

Fig. 18 – The top graph displays the distribution of participant error by the negative gorilla stimulus viewed. Participants reported a perceived gaze reversal in ≥ 15 trials in the above five negative stimuli pictured. Participants reported a perceived gaze reversal most frequently in gorilla stimulus g13/g32 (top right stimulus, 37 errors).



These negative orangutan stimulus examples are unavailable due to copyright restrictions.

Fig. 19 - The top graph displays the distribution of participant error by the negative orangutan stimulus viewed. Participants reported a perceived gaze reversal in ≥ 10 trials in the above four negative stimuli pictured. Participants reported a perceived gaze reversal most frequently in orangutan stimulus o3/o13 (top right stimulus, 29 errors).



These negative bonobo stimulus examples are unavailable due to copyright restrictions.

Fig. 20 - The top graph displays the distribution of participant error by the negative bonobo stimulus viewed. Participants reported a perceived gaze reversal in only these three negative stimuli pictured. Participants reported a perceived gaze reversal most frequently in b3/b8 (top right stimulus, 27 errors).

3. Original Bogart stimuli

Overall, participants responded quickly (*mean RT* = 702.9 ms) and accurately (*accuracy* = 99.1%) to the Bogart stimuli in positive polarity. Only two errors were committed out of the 223 positive participant responses, corresponding with Sinha's (2000) original results. Error increased significantly, but only slightly, when the polarity of the stimulus was negative (*error* = 7.6%, $n = 16$; $\chi^2_{(1)} = 12.3$, $p < .001$) and participant response time slowed (*mean RT* = 935.4 ms). The difference between RTs for the positive and negative polarities was significant (*Wilcoxon-signed ranks test*: $z = -4.4$, $p < .001$) with faster RTs occurring when viewing positive polarity Bogart faces (see Table 8: I). However, only 12 of the 28 participants made any response errors when viewing negative Bogart faces and the highest number of errors for any one participant was 3 out of the 8 total negative stimuli viewed (Fig. 21).

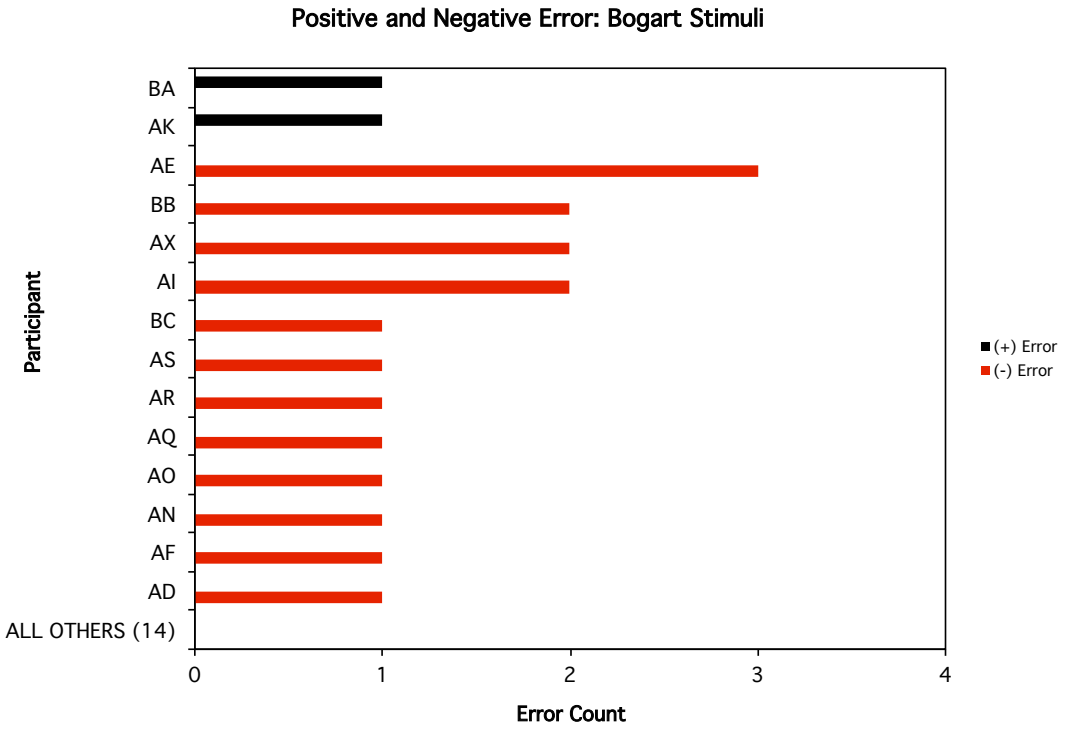


Fig. 21 - The above graph illustrates participant response errors (counts) for positive and

negative Bogart stimuli. The perception of a gaze reversal in negative Bogart stimuli was infrequent; instead, the majority of participants demonstrated 100% accuracy in gaze judgments when viewing either polarity ("all others" label).

Discussion

The aim of this experiment was to investigate the low prevalence of the Bogart effects shown in Experiment 1, which contrasted with the results of the original study (Sinha, 2000). The main objective of this study was to determine whether methodological differences between this study and the original contributed to the discrepancy between the studies; namely, whether the use of direct gazes, a third response option (center), and the eye-region specific ape and human stimuli of Experiment 1 were responsible for the unexpectedly low Bogart effects. To address these differences, Experiment 2 eliminated direct gazes, discarded the center gazing option, and included the full-face Bogart stimuli of Sinha's original study. Using only averted gazes, I again explored whether gaze information was available to a human observer when judging gaze direction in dark sclera eyes and whether dark and light sclera apes and human eyes generated Bogart effects.

1. Gaze direction judgments: positive polarity stimuli

Similar to the results of Experiment 1, participants responded accurately to all four stimuli groups (dark sclera apes, light sclera apes, humans, and Bogart faces) when presented in positive polarity. The high accuracies of both Experiments 1 and 2 when viewing light sclera stimuli remained consistent with Sinha's (2000) results of 100% positive polarity accuracy. Participants again excelled at quickly determining the gaze direction of both human and light sclera apes, confirming the results of Experiment 1 and

further emphasizing the human capacity to efficiently and quickly discern gaze direction among our own species (Ando, 2002) and light sclera apes when only provided with the eye region. This result also suggests that a light sclera effectively contributes to gaze direction determination, regardless of a human or non-human ape source.

1.1. *Dark sclera*

More clearly than Experiment 1, Experiment 2 demonstrated that the absence of a light sclera did not mean the absence of local eye gaze information. Participants responded with significant accuracy when viewing dark sclera eyes, and in fact, the dark sclera accuracy level for Experiment 2 (95.9%) was higher than the accuracy shown for dark sclera averted gazes in Experiment 1 (60.3%). Additionally, responses to dark sclera gazes in Experiment 2 were faster (720.4 ms) than the averted gaze RT of Experiment 1 (924.9 ms). Our results suggest that although an observer may take slightly longer to respond to a dark sclera stimulus, they are still capable of using the available gaze information to correctly determine the gaze direction in that stimulus. A longer mean RT in comparison to light sclera counterparts (humans, light sclera apes, and Bogart stimuli) may be attributed to the fact that light sclera confers the observer a slight temporal advantage in gaze direction determination. However, based on the high levels of accuracy for dark sclera apes in this experiment, a light sclera does not appear to be a requirement for the accurate detection of gaze. Overall, the low amounts of error when any naturalistic ape eyes were viewed suggests that sufficient gaze information is available in the eye region of apes, whether light or dark, for exploitation by at least a human observer.

Therefore, the results of Experiment 2 do not support the cooperative eye hypothesis assumption that a dark sclera eye is inadequate for accurately conveying gaze information based on its uniform coloration. These results also indicate that for human observers, dark sclera does not necessarily have a gaze camouflaging effect, at least in the laboratory conditions in which these stimuli were presented. Having a light sclera trait may therefore be an added gaze-enhancing cue that plays an important role in a more naturalistic setting where ambient lighting, viewing distance, and other environmental variables bear influence on gaze judgments.

2. Bogart effects: negative stimuli

Our overall results were not as robust as Sinha's (2000) for the perception of a Bogart effect in our light sclera stimuli (human eye-focused, light sclera apes, and Bogart faces). Surprisingly, Experiment 2 shown even less of a light sclera effect than Experiment 1 even with the inclusion of the original Bogart stimuli, which generated only 7.6% perceived gaze reversal. The perception of the illusion for these original full-faced Bogart stimuli was even lower than the Bogart effect reported for the eye-focused human stimuli of this study (13.5%). Those participants that reported a reversal in gaze only did so in low amounts (12.5-37.5% of the overall viewed Bogart faces), which differed greatly from the 60-80% reversal per participant of the original study (Sinha, 2000).

Light sclera apes significantly generated more of a Bogart effect than the human stimuli; however, the amount was comparable between the three light sclera ape species (bonobo, gorilla, and orangutan), which indicated that participants did not perceive a greater reversal effect in any particular species. In comparison to human stimuli, the

significantly higher frequency of a Bogart effect in light sclera apes may have been due in part to the variable skin and hair color differences observed in the non-human great apes. Darker facial skin would contrast heavily with any lighter area of the eyeball and could contribute favorably to any existing light/dark contrasts. In this regard, any visibly lightened areas would "pop" more against a darker ape face (Fig. 22).

These examples of a chimpanzee and human face are unavailable due to copyright restrictions.

Fig. 22 – The orbits and surrounding facial skin of the chimpanzee (**top**) and human (**bottom**), including the brow ridge and eyebrows in both species.

It is plausible that the results from Sinha's study were anomalous and most participants do not actually perceive the "Bogart illusion" on contrast inversion. It is also possible that a specific set of circumstances is necessary to produce the Bogart illusion. Our results indicate the former, as the same stimuli of the original study were also used in Experiment 2, and the majority of participants (n = 16) did not perceive the "Bogart illusion" at all from these stimuli. Therefore the disparity in the results should not be inherent to the stimuli used. The presentation of the stimuli was random dispersal in both this and the original study, thus the presentation order should also have had no influence on the perception of a contrast illusion. It is possible that the experimental procedure of Experiment 2 played an influential role in participant response because these full-face

stimuli were presented randomly with the eye-focused stimuli, thereby minimizing any facilitating effect that full-face stimuli may have had in the original study.

2.1. *Methodology differences*

The discrepancies in the results of Experiment 2 with other previously effective contrast reversal studies may lie with methodological differences. In particular, Experiment 2 used "eye-focused" stimuli as opposed to whole faces (Olk *et al*., 2008, Ricciardelli *et al*., 2000; Sinha, 2000). The entire stimulus (the eyes and surround) was also negatively contrasted, which remained consistent with the original study (Sinha, 2000). Some contrast studies have only contrast reversed the sclera (Ando, 2002; Olk *et al*., 2008; Ricciardelli *et al*., 2000) and left the remainder of the stimulus in positive polarity. This more localized and eye-specific contrast methodology may provoke a different perception of the stimulus gaze, as the entire stimulus is not novelly affected by negative polarity.

An additional methodological consideration for observing less of a Bogart effect in Experiment 2 may have been the elimination of the center response option (present in Experiment 1) from the methodology of Experiment 2. Although this manipulation was originally intended to eliminate potential difficulties in provoking the Bogart effect, it may have produced the opposite effect. In Experiment 2, the participants were only provided with two discrete response choices, left or right, thus reducing any ambiguity introduced by the possibility of a center choice. This was demonstrated, in particular, by the dramatic reduction of dark sclera ape positive error between Experiments 1 and 2. Repeatedly in Experiment 1, participants erroneously reported the gaze direction of this stimulus group as being center-oriented. The removal of the center response choice in

Experiment 2 yielded results that were better defined and more accurate overall, echoing the results of previous polarity studies with human stimuli (Olk *et al*., 2008). It appears that when presented with two discrete response choices, such as left or right, participants can judge gaze direction in unfamiliar stimuli more efficiently, quickly, and accurately. However, when presented with a more subjective choice such as center, in addition to the presentation of a novel stimulus, the gaze direction judgment became slower and more prone to error. This is a valuable methodological consideration for future contrast inversion studies, as participant responses can be greatly shaped by the available response choices. While a two-choice response system is methodologically cleaner and perhaps more easily interpretable, a multi-choice response system, including a direct gaze option, may be more ecologically valid. Certainly, determining whether one is the focus of another's attention is considered to be a key function of gaze detection, and direct gazing stimuli would reproduce this (Bard *et al*., 2005; Emery, 2000; Farroni *et al*., 2002). Although it may provide messier results, multi-direction stimuli and multi-choice options would allow for richer and more ecologically valid interpretations of the data.

General Discussion

The idea and application of a light/dark contrast rule as part of the visual system's process for determining gaze direction merits further investigation in humans, primates, and other mammals. Our studies made use of this contrast principle to further investigate the cooperative eye hypothesis and the contribution of light sclera to accurate gaze direction judgments. This application using naturalistic light and dark sclera great ape eyes, human eyes, and full-face Bogart stimuli allowed for comparisons between sclera

coloration and between human and non-human great ape categories. The results of both Experiments 1 and 2 were consistent with one another and suggest that when available, light sclera is a valuable contributing cue for enhancing eye gaze direction in humans. Our studies provide new evidence for a light sclera benefit in the great apes and also demonstrate that in the absence of this gaze cue, local eye gaze information in all-dark ape eyes remains available for accurate gaze direction judgments. Therefore, our results suggest only partial support of the cooperative eye hypothesis; all-dark great ape eyes do not lack gaze information, although the addition of a light sclera cue enhances the gaze information that is available. To determine gaze direction in any of the stimuli, participants may have possibly drawn on a few of the available features of the eye region.

1. Luminance contrasts and facial cues

The luminance levels within the eyeball – the variable contrasts between the iris and sclera color – differed between individuals and species but were still available in dark sclera eyes although they were present to a much lesser degree than light sclera counterparts. Any such degree of contrast within the eyeball would be useful to enhance specific geometrical outlines (e.g., the iris within the sclera and eye outline within the surrounding face) and could be evaluated similarly to starker light/dark contrasts are judged in light sclera individuals.

Expanding outwards, the face consists of much more than just a pair of eyes and a light/dark heuristic to evaluate them. A cursory comparison between the faces of humans and non-human great apes reveals some noticeable anatomical differences; a multitude of features, such as the location of the eyebrows, level of the cheekbones, orbit direction,

nasal direction, and elevation and direction of the head, can provide congruent or conflicting directional information that can either help or hinder the ability to correctly assess gaze direction. The great apes have a pronounced brow ridge, more concave orbits, and facial skin framed by hair that connects to the hair on the rest of the body. Conversely, humans have a reduced brow ridge, a horizontally elongated eye outline (Kobayashi & Kohshima, 2001; this thesis Chapter 2), and variable lines of facial hair on both the top of the brow ridge and occasionally on the lower half of the face in men (Sadr *et al*., 2003). The eyebrows offer a high contrast line in comparison to the rest of the face and have been proposed to play a necessary role in facial expressions that convey emotions and other social signals (Tipples, 2005). Research has shown that familiar face recognition decreases dramatically when the face is shown without eyebrows; in fact, participants were significantly worse at recognizing faces without eyebrows than they were at recognizing faces that lacked eyes (Sadr *et al.*, 2003). Therefore, the location and angle of the eyebrow on the brow ridge may add additional contextual information about the location and general direction of the eyes by providing an upper boundary for the periocular region. When a stimulus is presented in negative polarity, additional facial information could potentially reveal the "true" gaze of a stimulus, and through the application of this cue, participants may be "fooled" less frequently by any contrast illusions. The location of the eyebrows would be particularly salient in humans where the eyebrows typically contrast heavily with the rest of the face. If eyebrows are a particularly useful cue, the opposite reasoning would be applicable to the great apes, and their minimization on ape faces would generate a more uniform contrast around the eyes that potentially opens participants up to the possibility of being "fooled" more often.

However, the role of eyebrows in gaze direction judgments of humans and great apes must be investigated because of the variability of eyebrows among the species.

2. Light sclera

Some speculation can be made concerning the universal presence of a light sclera characteristic in humans with human communication being a pivotal motivator for the selection of this trait. Both Experiment 1 and 2 demonstrated that the advantages of possessing a light sclera are associated with increased gaze judgment accuracy and decreased RT, which for humans may be of importance. It can be hypothesized that an exchange between humans includes more than a face-to-face discourse and additional information about the surrounding environment is also of equal relevance. A conversation would therefore benefit from alternations between the eyes and face of a partner with a specific event or object in the environment. This would enhance the understanding that the communication occurring is about a specific environmental element, and the possession of a light sclera would contribute to this understanding both quickly and precisely. Direct gazes in particular would benefit from the addition of a white sclera, increasing the light contrast around a dark and centered iris. The facilitation of direct gaze detection would be valuable for human communication by quickly informing an individual of when they are the object of another's attention and communicative interaction. Experiments 1 and 2 also demonstrated that a light sclera contributed to gaze direction detection regardless of the novelty of the gaze stimulus viewed, as the effect was detectable for humans that viewed ape eyes with natural light sclera. Conceivably, the effectiveness of light sclera is therefore amplified by the instrumental foundation of already existing gaze information, which is present in dark

sclera eyes. Therefore, having the ability to recognize and use existing gaze cues under degraded viewing conditions would only enhance the ability to use such cues in an optimal setting, i.e., in eyes with greater contrast ratios. The results also demonstrate that at the eye region, directionality cues exist beyond a light sclera and dark iris contrast. Although humans are considerably more accustomed to using this salient contrast and naturally have a greater familiarity with its existence, they are still capable of processing gaze without this particular characteristic.

One study consideration that should be addressed in future work is a repetition of the study using great ape species as the participants. Currently, these results are only applicable to a human observer. It is possible that humans have developed a particular sensitivity to a variety of gaze cues, and therefore a comparison with the results derived from great ape participation would draw different conclusions.

An investigation using great apes as observers would allow for the further evaluation of the cooperative eye hypothesis, and a few conjectures in relationship to this hypothesis can be made. Primarily, if great apes were shown to reliably follow the eye gaze of all-dark eyes and exhibit improvement in the presence of a lightened sclera, then light sclera again confers an advantage that builds on already existing gaze-following skills. These skills more importantly would rely on local eye cues, which would oppose the proposal of the cooperative eye hypothesis that apes rely more on head cues. Secondly, if a light sclera is not observed to confer any gaze accuracy benefits to the great apes, then light sclera may just be one adaptation specifically evolved by humans amongst a wider suite

of cues for enhanced gaze detection. This suggestion then leads to the further inquiry of why apes with varying degrees of natural light sclera exist in wild and captive populations. Following the propositions of the cooperative eye and gaze camouflage hypotheses (Tomasello *et al.*, 2007; Kobayashi & Kohshima, 2001), great apes with this characteristic would be expected to be at a significant disadvantage. However, the exploratory review of a light sclera characteristic in gorillas in Chapter 2 noted that this trait appears to occur with some frequency within the species. Wouldn't these individuals be considered to be at a disadvantage in comparison to their all-dark eye peers? It is entirely possible then that such a characteristic is superfluous and offers neither a substantial advantage nor disadvantage because the phenotype has been neither selected for nor eliminated in the great apes.

In general, the results of Experiments 1 and 2: 1) demonstrate the human ability to efficiently utilize local eye information, even when presented with such novel and unfamiliar stimuli as ape eyes; 2) suggest that while conspicuous light/dark contrasts may help enhance gaze direction, it appears that they are not a requirement to interpret gaze direction (at least for human observers). The light and dark heuristic may therefore be overvalued, as examples of eyes with low levels of contrast appear to provide enough information for participants to determine gaze direction; and 3) indicate that a light sclera, that was reported for gorillas in Chapter 2 and illustrated in this chapter by the inclusion of naturalistic stimuli examples, may offer the same functional capacities in apes as it does for human eyes (to at least a human observer). The results of this chapter further reinforce the light sclera results of Chapter 2, which weaken the gaze camouflage

hypothesis (Kobayashi and Kohshima, 2001) for dark sclera ape eyes. However, these results also simultaneously emphasize that the presence of a light sclera did not confer enough of a significant gaze advertising advantage to the great apes to be a trait that is maintained as ubiquitously throughout the species as it is for humans.

CHAPTER 4:

The role of attentional cues during vigilance periods in the social play behavior of captive western lowland gorillas (*Gorilla gorilla gorilla*)

Chapter 4: The role of attentional cues during vigilance periods in social play behavior of captive western lowland gorillas (*Gorilla gorilla gorilla*)

Introduction

The previous chapters (Chapters 2 and 3) addressed questions about the local eye information available in ape and human faces when determining gaze direction in another individual. I showed that gaze information that is available in the great apes is not limited to head or body direction, but is also prevalent in the typical dark sclera eyes. The evaluation of gaze information in isolation of supplementary facial, head, and body information shows that dark sclera eye gaze contains cues about gaze direction for at least a human observer. Nevertheless, when isolated to only the eye region, gaze cues cannot be reduced to simple algorithmically computable cues, such as luminance ratios or white/dark contrasts; the configural interaction of the surrounding facial features, such as the eyebrows, the nose, etc., may play a role in the advertisement of gaze direction. Gaze is consequently an increasingly complex category subserved by the amalgamation of an assortment of cues.

However, the results of those studies were based within a controlled and experimental context using 2D eye images, some of which would only exist within an artificial environment (for example, the cropped and modified photographs showing only the eye area of an individual). While the experimental approach allowed for the isolation of the eye gaze cue and a more technical analysis of eye gaze components, an experimental method leaves little room to evaluate the practical and dynamic display and use of eye gaze and other attentional cues during naturalistic social interactions. The aim of this

chapter is to explore how gorillas display and use attentional cues in a naturalistic, affiliative social interaction – social play.

1. Play behavior

The literature has produced a considerable number of varying definitions of play behavior that strive to clarify what actions fall under the heading of play and how scientists can confidently identify the actions being observed as play. Specific criteria have been developed that when applied to an observed behavior and when simultaneously fulfilled – either partially or in their entirety – can distinguish play from other common behaviors. In short, these criteria suggest that play has a limited immediate function, is endogenous, maintains structural or temporal differences from "serious" behaviors, is repeatable but not stereotypical[11], and is performed in a relaxed field (see Burghardt, 2005, pg. 70-81). When applied conscientiously, these criteria can aid in determining whether a specific behavior or behavioral sequence is playful; however, little attention has been paid to establishing the quantitative timeframe where play is said to begin and end. This component of play research has received little explicit mention; however, such a timeframe appears to be a critical component in understanding more about play in general.

Juvenile great apes have an inclination to be explorative, curious and sociable, as observations on ape social interactions demonstrate (Fossey, 1979; Harcourt, 1979;

[11] Stereotypical behavior is "a behavior pattern that is repetitive, invariant, and has no obvious goal or function", best exemplified in captive animals (Mason, 1991) e.g., the incessant pacing of big cats and bears within some zoo enclosures. While this definition appears to satisfy some of the criteria characterizing play, stereotypical behaviors are repeated, rigidly formatted and are used as a typical welfare indicator signifying distress.

Schaller, 1963). Play behavior, in particular, derives from the interface between innate curiosity and exploration and the surrounding environment and group mates. Additionally, both experimental and observational research has shown that great apes have the propensity to be aware of attentive versus inattentive conspecifics (Liebal *et al.*, 2004; Pika *et al.,* 2003; Poss *et al.*, 2006), a comprehension that would be significant for successful social interactions. In play, deciphering the difference between an attending, receptive play partner and an inattentive, uninterested partner would determine whether the partners are likely to engage socially. Therefore, the examination of social play behavior provides an optimal arena to investigate the role of social attention between interacting individuals. Western lowland gorillas (*Gorilla gorilla*) have extensive play behavior repertoires (Hoff *et al.*, 1981; Gorilla Behavior Advisory Group ethogram collection, 1991), spanning varied types of play patterns (e.g., object, solitary, locomotive, and rough-and-tumble) across various playmate age groups (Fossey, 1979; Schaller, 1963, Watts and Pusey, 1993). Play behavior research has focused primarily on deciphering the function and immediate versus long-term benefits for the individuals involved (Palagi *et al.*, 2004 & 2006). While multiple hypotheses have been suggested for this distinctive collection of behaviors (**physical/motor-training skills**: Byers and Walker, 1995; Fontaine, 1994; Martin and Caro, 1985; Smith, 1978 & 1982; **socialization:** Bekoff, 1972; Brown, 1988; Martin and Caro, 1985; Poirier and Smith, 1974; Smith, 1978 & 1982; **cognitive/sensorimotor training [behavioral flexibility]**: Bekoff, 2001; Martin and Caro, 1985; Palagi *et al.*, 2007), a cohesively unified scientific explanation outlining an ultimate function has not yet been achieved. Naturally, depending on the areas of personal scientific interest, debate arises when promoting

which aspects of ontogeny play nourishes. However, the dominating prevalence of play across the majority of mammals (although not exclusive to) has play researchers exploring various niches in attempt to cohesively unify the current literature and foster a better understanding of what, why, and how animals play. Many authors do however reach the consensus that play is one of the most sophisticated manifestations of social communication (Bekoff, 1972, 1997; Burghardt, 2005; Fagen, 1981; Pellis and Pellis, 2009). In more recent play research, particularly in canines and primates, interest has grown in the exploration of the complex relationship between socio-cognitive development and the behavioral flexibility derived from social play (Palagi *et al.*, 2007; Pellis and Pellis, 2007; Tanner and Byrne, 2010; Udell *et al.*, 2011).

2. Vigilance periods

The majority of socio-cognitive primate play research has focused on interpreting the use of play-specific signals, which when used, are said to signify and reinforce to the partner that the interaction they are engaged in is a playful one (Flack *et al.*, 2004; Palagi, 2006, 2009; Palagi and Mancini, 2011; Pellis and Pellis, 1996, 1997, 2011; Pellis *et al.*, 2011; Waller and Dunbar, 2005). However, little investigation has been made into the more general and subtle cues that indicate attention direction and orientation outside of these conspicuous and often unique play signals. Anyone that has spent time at the primate house at the zoo or witnessed an impromptu play tumble between pets can appreciate that a play bout is composed not only of playful behaviors but also of intermittent lapses in activity. These moments of downtime – sometimes lengthy, sometimes brief – where play partners are seemingly inactive may actually instead be moments of rich attentional exchanges, partner assessments, and situational interpretations rather than brief social

disengagement. It is within these time frames that gorillas may be gathering information about the attention and intentions of their partner through the observation of a variety of social cues.

The present chapter places its main focus on the periods of time during social play bouts when actual play was not occurring. To our current knowledge, no research has been conducted explicitly on these time frames, which in gorilla play occur as periods of rest or intervals between play periods. From here onward, these intervals of time are designated as **vigilance periods** or **VPs** for brevity. To further clarify the structure of the interaction evaluated within this study, the term *play bout* denotes an entire playful interaction between partners from initiation to termination, encompassing both play time frames and VP time frames. A *"period"*, of either vigilance or play, denotes that particular instance, i.e., a play bout is made up of many smaller play periods and vigilance periods. It should also be noted that the use of VP in this study is different from the *vigilance behaviors* that many primates engage in, which specifically monitor for external predatory threats (Breed and Moore, 2012). In accordance with Burghardt's (2005) criteria, play is mutual, voluntary, and occurs in a relaxed environment; VP vigilance is therefore less about a concern for serious external events and more about interdependent dyadic engagements with a play partner.

2.1. *Development of an operational definition of play periods and vigilance periods*

Many play researchers have provided provisional play definitions and criteria to abide by, but an operational definition that can be applied systematically when observing play has yet to be devised. Furthermore, the play literature has lacked a discussion of VPs, and

thus a formal definition for a VP has not been achieved. One aim of this study was therefore to provide a clarification for play and VPs and to formulate a method with which to distinguish the boundaries between the interaction types based on behavioral observations.

The exact moment that play is initiated or terminated between two play partners is difficult to objectively measure, particularly when considering the variable nature of play behavior itself. Since VPs occur as a result of a break in a playful interaction, the boundaries between play and VPs are inherently contingent on one another. However, distinguishing definitively between the beginning and end of these two behavioral periods poses a relatively subjective task to the observer. One consideration for differentiating between VPs and play periods is how the proximity of play partners to one another changes throughout the interaction. Every animal and object occupy an area of "space" within the environment, and the relationships between these spatial areas are in a state of constant fluctuation as an individual navigates through the environment. The study of *proxemics* in the 1960's was the beginning of a movement in anthropology investigating human's cross-cultural use of space (Hall *et al.*, 1968). Humans place a heavy emphasis on the management of spaces, which is exemplified from a young age at school where children are constantly reminded to respect and stay out of the "personal space" of others. Additionally, we are wary when a violation of our own personal space occurs, although we may not react based on preconceived quantitative boundaries, but rather based on subjective personal comfort levels. Violations of these boundaries can facilitate either a positive or negative reaction depending on the relationship with the

violator (familiar vs. stranger), the interaction state prior to the violation, and the interaction state on continuation of the interaction after the violation. Ethologists make similar judgments of proximity distances between interacting animals when conducting behavioral observations. Play often spans all levels of proximity between partners, from continuous direct contact during rough-and-tumble to the greater expansions during chase play. Therefore, noting the changing distances between individuals may be valuable addition for a definition of play since the observable changes in spatial relationships could be informative about the characteristics of the interaction between the partners.

Observations of play have shown that specific behaviors often occur in high correlation with play, which may either initiate a bout between partners or, through repetition and precise timing within the play interaction, reinforce that the context of the interaction is playful (e.g., the play bow in canids [Bekoff, 1995] and the open mouth face in primates [Waller and Dunbar, 2005]). The observations of these signals have therefore been used in observations of play to recognize play from other non-playful contexts. While these signals can certainly be a part of the play repertoire, some research has indicated that they do not provide an unambiguous indication of play because of their variability in form, frequency, and temporal occurrence during play (Pellis and Pellis, 1996; Pellis *et al.*, 2011). Therefore, for this study, play signals were excluded from the working definitions to diminish any observational reliance on them as specific indicators of play. Gorilla vocalizations were also excluded from the following definitions because the gorillas were not within an audible range to accurately record play vocalizations.

2.1.1. *Play and VP definitions*

Burghardt's (2005) criteria (section 1, pg. 132) used to define playful behaviors provided the foundation for the following definitions. For coding the behavior sequences of this portion of the thesis, the operational definitions outlining the margins of play periods and VPs established for this particular study were as follows:

Play begins *when gorilla A moves into gorilla B's space in such a manner that*: 1) *the physical proximity between the gorillas changes (depending on the play pattern observed);* 2) *the gorilla's locomotion changes in tempo or pattern toward "play";* 3) *either gorilla displays behaviors of an exaggerated, spontaneous, or repetitive format; and* 4) *the behaviors and mannerisms of gorilla B are reciprocal to those of gorilla A.*

The definition for the beginning of play relies on the characteristics of the locomotion of the gorillas and the exhibition of behaviors that fit the criteria of play. The proximity change between partners is naturally variable from interaction to interaction; in the case of the initiation of contact play, locomotion is typically toward a partner and increases the proximity, while in the case of initiating chase play, locomotion is typically away and may decrease proximity.

Play breaks and a VP begins *when*: 1) *the exhibited playful behaviors cease;* 2) *both gorillas remain within visual range of one another and at a distance such that an interaction can be re-engaged* (*~3 m or less*)*; and* 3) *either gorilla withdraws from the other's space* (≥ *1 m*) *and remains withdrawn for ≥ 1 second, OR both gorillas mutually*

withdraw away from one another.

Similarly to how play begins, a break in play also varies depending primarily on the type of play pattern the dyad is engaged in and the proximity of the partners. To identify a distinct and observable end point, play was said to break at the moment where the gorillas withdrew from one another in space. This was regardless of whether they kept withdrawing from one another, e.g., gorilla A may walk away to withdraw from gorilla B; however, the "walking away" behavior was not included as a part of play. The withdrawal behavior performed was instead included as a VP behavior because 1) a withdrawal indicates a break in the reciprocity of the interaction, reciprocity being one of the measures of play behavior; 2) the diversity of locomotive movements that could be used to satisfy withdrawing from a partner; and 3) the variability in the amount of time it took to withdraw. Withdrawal was therefore not determined by duration or discrete proximity measurements between play partners; its occurrence simply marked the boundary between a play period and VP (e.g., gorilla A ceases to participate in wrestling by sitting down). Additionally, the interaction distance between gorilla partners (criteria 2) was established at ~3 m or less based on the constraints of the enclosure and observer.

VP ends *when either A)* ***play begins*** *and gorillas resume play as defined in the "play begins" definition above; OR B) the particular dyadic* ***play interaction terminates*** *when:* 1) *a 3rd party joins the interaction;* 2) *the exhibited behavior pattern transitions into aggression, grooming, or sex;* 3) *either gorilla withdraws from the space* (≥ 1m) of *the other and moves out of visual range of the partner;* 4) *either gorilla moves and remains*

out of visual range of the observer (*i.e., the observer cannot move to an alternate location around the exhibit to re-establish visual contact*).

The boundary indicating the end of a VP and the re-engagement of play lies at the exhibition of any re-engagement behavior, which naturally fulfills the criteria indicating play and typically decreases the space between the partners. The interaction can also terminate altogether, either after engagement in a VP or immediately after play (Fig. 23).

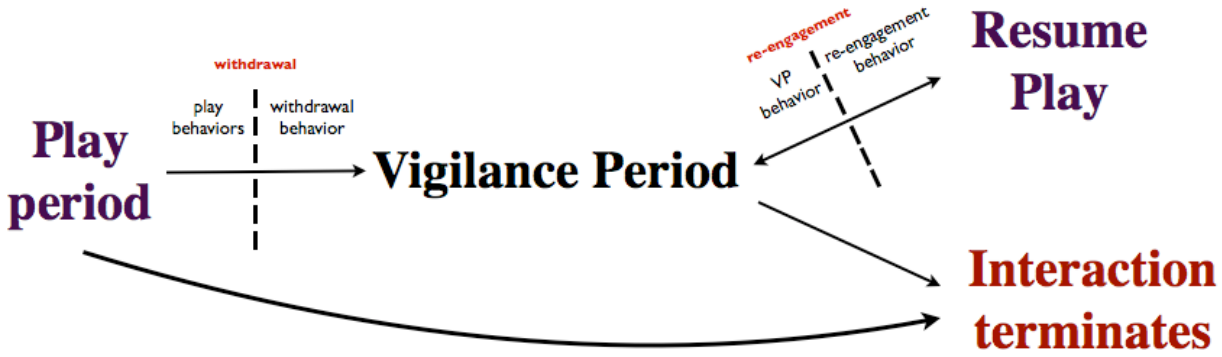


Fig. 23 – The potential flow between play periods and vigilance periods ending in either the resumption of play between partners or termination of the interaction.

3. Study aims and summary

The beginning and end points of both play periods and VPs are dependent on one another, and the cyclical and interdependent nature of their definitions highlights how partners can transition from one to the other fluidly and quickly. One of the main objectives of this portion of the research was to determine the types of social cues available to play partners and to investigate their influence on navigating playful social interactions. The rationale of this study was that to navigate the complex dynamics of play engagement, vigilance periods, and play re-engagement or termination, gorillas would need to take into account both attentional and intentional signals expressed by

their bodies and behavior. However, this study was not an examination of the cognitive mechanisms through which these signals are processed, but rather, the aim was to record what signals are available (gaze direction and body orientation), which appear to be actually used by the gorillas, and how these cues work within the dynamics of the interaction. The study specifically focused on the attentional cues of eye gaze, head orientation, and body orientation in relationship to each gorilla in the play dyad. These cues may be one way that gorillas collect general social information that can be easily exploited to identify the participation level and intentions of a partner.

VPs were deemed to be ideal situations to analyze the cues that gorillas use to both express and react to attentional and intentional states with a partner. As VPs reflect moments of rest or pause in play that may or may not resume, partners might pay particular attention to one another to anticipate the progression of the interaction. The specific orientations of these cues throughout a VP could potentially contribute to the continuation or termination of the interaction and may help each individual make decisions about continuing or abandoning play with their partner.

This study also involved a comparison of two interaction types, VPs and non-play restful periods, with the aim to explore the similarities and differences in how attentional cues are used by gorillas throughout interaction types with differing social contexts. This comparison of interaction types aimed to determine if VPs were indeed "special" in terms of the amount of attentional information displayed and gathered, and ultimately discuss: 1) how attention is used and structured during VPs and whether this differs from non-play

rest interactions, and 2) whether VPs can be set apart from other types of social interactions and therefore be considered unique expanses of time specific to the play context. It is predicted that VPs are in fact, special and crucial components of play and that attentional cues are used differently and are more partner-directed in comparison to non-play restful interactions.

Methods

1. Study site and gorillas

The study site was the indoor "Tropic World" exhibit at the Brookfield Zoo in Chicago, IL, USA. The gorilla exhibit was an irregular shaped grotto approximately 33 m long by 27 m wide. The exhibit floor varied from 7 to 11 m below a public walkway that surrounded the entire perimeter of the open-air enclosure. The enclosure contained an artificial mountain with its peak at eye-level with the public walkway. The mountain was equipped with artificial trees, ropes, and a hanging plastic ball. The base of the mountain was surrounded on three sides by a dry moat; a waterfall and river ran down into a pool on the fourth side. The water pool flowed from the gorilla enclosure into the adjacent enclosure separated only by mesh wiring, which allowed for both visual and audible access into the adjacent enclosure that housed Red-Capped Mangabeys, Colobus monkeys, Mandrills, and a pygmy hippopotamus.

The study group consisted of seven western lowland gorillas (*Gorilla gorilla gorilla*) ranging from 4 years to 41 years of age (female: $n = 4$, male: $n = 3$). The group was composed of 3 juveniles, 2 adolescents, and 2 adults (Fossey, 1979; Watts and Pusey,

1979). With the exception of the silverback Ramar, all individuals were captive born.

Name	Sex	Age	Age class	Birth
Ramar	M	41	Adult	Wild
Binti Jua	F	21	Adult	Captive – March 1988
Koola	F	14	Adolescent	Captive – February 1995
Bana	F	14	Adolescent	Captive – March 1995
Nadaya	M	8	Juvenile	Captive – April 2001
Kamba	F	4	Juvenile	Captive – May 2005
Bakari	M	4	Juvenile	Captive – May 2005

Table 18 – Pedigree information of the seven Brookfield Zoo (Chicago, IL) western lowland gorillas observed in this study.

2. Data collection

Data collection occurred from July-September, 2009. Behavior sampling was used to detect play activity and continuous recording was used to record play and VP data (Altmann, 1974; Martin and Bateson, 1993). Data were collected using a handheld Panasonic SDR-S26 HandyCam and the footage was uploaded into MPEG Streamclip (1.9.2) for conversion into .mov files. The videos were then played back and coded using a combination of Quicktime Player (MacOSX, 10.0), MPEG Streamclip and Microsoft Excel.

3. Non-play restful controls

In addition to the collection of VP data, data on non-play restful scenarios were also extracted from the video footage as a control comparison. For example:

> *Both Bakari and Nadaya are resting on alternate levels of the enclosure. Bakari stands up and walks to Nadaya sitting down 1 meter away. Bakari remains at rest while Nadaya eats hay. Bakari then rises and climbs down an enclosure level out of visual range of Nadaya.*

These episodes were differentiated from VPs as periods of "rest" in which the gorillas were observed to abstain from social interaction with a partner (with the exception of allogrooming) and had not engaged in play with one another immediately before the restful period. Resting was observed to end if the gorilla engaged in an interaction with a partner, a period was not considered to be rest if the individual engaged in play immediately afterwards, or moved out of visual range of the observer.

Such expanses of "restful" time included simply resting or an engagement in other common activities, such as grooming or eating. The gorillas were typically seated or laying within the enclosure during these expanses of time. The above example also portrays plausible activities of gorillas engaged in a VP. The only observable behavioral difference between the two interaction types is that play between partners had not been engaged in immediately before, during, or after restful episodes, therefore placing the gorillas of restful interactions and the gorillas engaged in VPs in two discrete social contexts. This was ultimately the purpose of a comparison of the two interaction types – to "control" for the presence of play – to examine the use of attentional cues during both interaction types. The comparison of these timeframes would highlight any similarities and differences between the two social contexts.

4. Attention categories and data analysis

Statistical analyses were performed in IBM SPSS 19.0. Three cues of attention and their combinations were recorded for each gorilla in the play dyad: eye gaze, head orientation and body orientation (determined by torso direction). The direction of attention for each cue was recorded in relationship to the partner (Table 19; illustrative examples in Fig. 24,

25, and 26).

Attention cue	Attention direction	Description
Eye, Head, or Body	**To**	Directed at the play partner from an angle of 5° away or less.
Eye, Head, or Body	**Away**	Averted from the play partner at an angle on the horizontal plane of greater than 45°.
Eye, Head, or Body	**Down**	Directed toward the enclosure floor.
Head or Body	**Semi**	Averted from the play partner at an angle of 45° or less and greater than 5° from the play partner.
Eye, Head, or Body	**NV**	Not visible to the observer.

Table 19 – The potential recorded directions of attention per attention cue. A head or body orientation that was averted from the partner gorilla by ≤ 45° but > 5° was considered to be at a "semi" orientation in relationship to the play partner.

Data for VPs and controls were collected for each attention cue at two fixed intervals: the beginning 1 second of the VP and the end 1 second of the VP. These one-second intervals established the start and end points of the attention dynamics that were subsequently analyzed. Both gorillas were then evaluated for the duration of the VP to determine changes in the direction of attentional cues as the interaction progressed from start to finish. This analysis recorded all attentional direction changes, to better understand the dynamic flow of attention that occurred during VPs. VPs could then be categorized for further analyses by noting the changes in attentional cues; for example, whether the gorillas maintained the same attention direction at the start and end of the VP or whether attention alternated between the partner and other environmental targets.

Fig. 24 – An illustration demonstrating the possible visible body orientations (direction of the torso) that were occupied by the gorillas during control and vigilance period interactions. All orientation directions were in relationship to the play partner and the arrows point in the direction of the gorilla's body orientation. Gorilla (A) depicts a **toward** orientation; gorilla (B) an **away** orientation; gorilla (C) a **down** orientation; and gorilla (D) a **semi** orientation.

Fig. 25 – An illustration demonstrating the possible visible head orientations that were occupied by the gorillas during control and vigilance period interactions. All orientation directions were in relationship to the play partner and the arrows point in the direction of the gorilla's head orientation. Gorilla (A) depicts a **toward** orientation; gorilla (B) an **away** orientation; gorilla (C) a **down** orientation; and gorilla (D) a **semi** orientation.

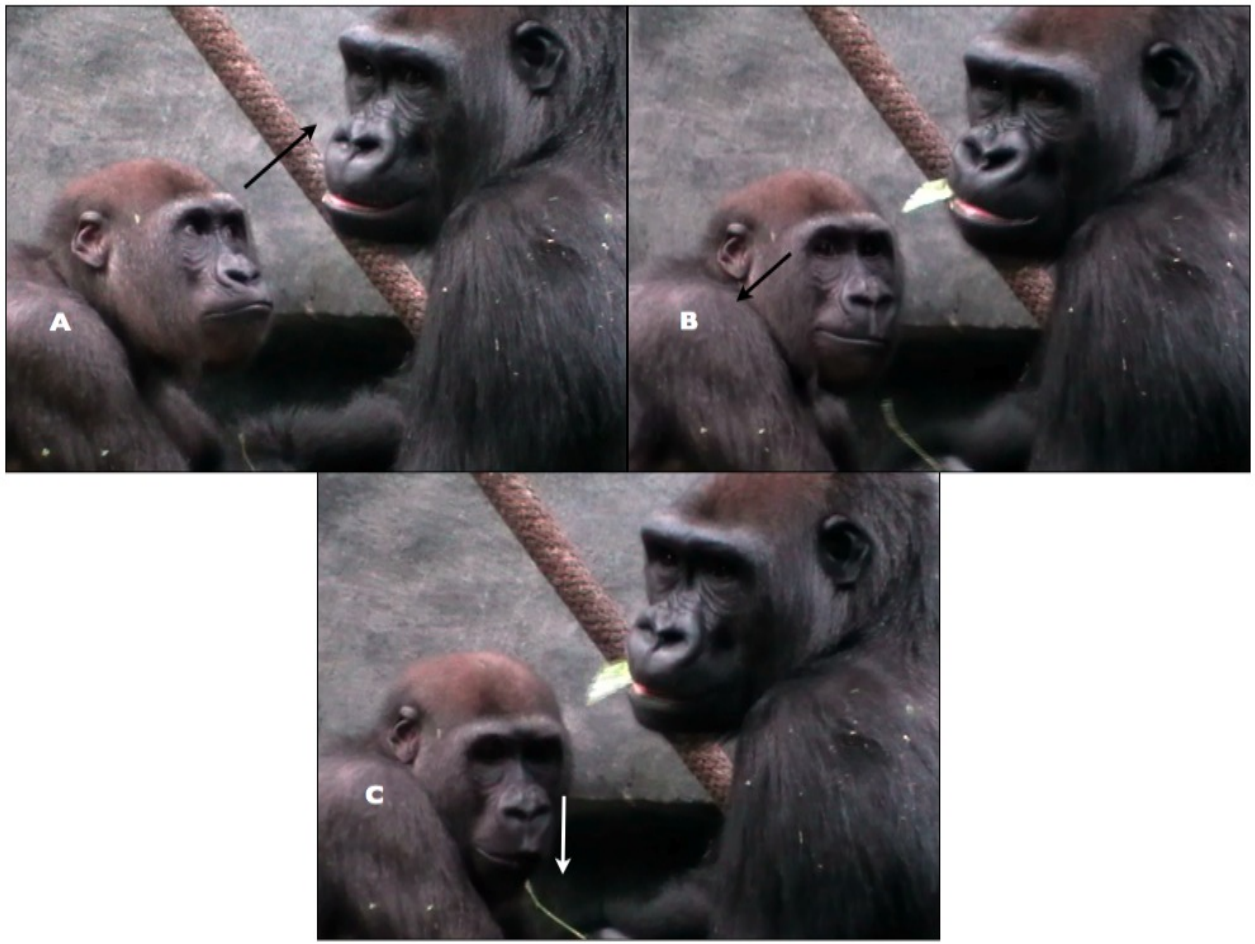


Fig. 26 – An illustration demonstrating the possible visible eye gaze orientations that were occupied by the gorillas during control and vigilance period interactions. All orientation directions were in relationship to the play partner and the arrows point in the direction of the gorilla's eye gaze attention. Gorilla (A) depicts a **toward** eye gaze orientation; gorilla (B) an **away** orientation; and gorilla (C) a **down** orientation. [Please note that in (B), Bakari is looking at the observer but the 2D arrow could not represent this; nonetheless, Bakari's gaze is directed away from his partner Nadaya.]

Data for both gorillas were further compared at each point of collection to investigate the overall attention of the dyad. "Dyad attention" categories were created for each of the three attentional cues (dyad eye attention, dyad head attention, and dyad body attention) based on the individual attention of each gorilla in relationship to their partner. Each super-category of dyad attention had four observable states: 1) both partners attending, 2) one partner attending, 3) neither partner attending, or 4) not visible to the observer (NV) [Table 20]. If the direction of any of the attention cues (eye, head, or body) for one gorilla was not visible (NV) to the observer, the dyad attention for that attention cue was also coded as NV, even if the observer could view the attention of the other partner.

Dyad attention	Description
Both partners ("mutual attention")	Both gorillas are attending to one another.
One partner	One gorilla is attending but the other is not.
Neither partner	Neither gorilla is attending to the other.
NV	Not visible to the observer.

Table 20 – The categories of attention of the gorilla dyad were the same four observable states for all three cues of attention – eyes, head and body. These categories for dyad attention were based on the individual attentional state of the gorillas in relationship to their partners.

All data were input into and analyzed in SPSS 19.0 (IBM). An initial analysis was conducted on the VPs to determine whether attentional direction, in relationship to a partner gorilla, changed from the beginning of the VP to the end of the VP. **Attention realignments (ARs)** were recorded when a gorilla averted their attention (either eye, head, or body) from the partner and then in the ensuing progression of the interaction, realigned their attention back toward their partner. ARs were only recorded as such after the gorilla averted their attention from their partner for the first time in the VP. For example, if gorilla A had their attention oriented towards gorilla B at the beginning of the

VP, gorilla A would need to avert attention from gorilla B and then any instance of realignment back toward gorilla A would be considered an AR. When an AR was performed, the directions of all three cues of attention were recorded for both partners.

In some instances, a gorilla may not have participated in ARs if they remained oriented toward their partner for the duration of the VP. Some VPs without attention realignments might, however, contain **attention transitions (ATs)**, if the attentional cue during these particular instances "transitioned" either toward or away from the partner without a subsequent realignment. For example, if gorilla A had their attention oriented away from gorilla B at the beginning of the VP and then reoriented their attention toward gorilla B at the end of the VP, this would be considered an AT. The beginning and end orientations of each attention cue – first body orientation, then head orientation, and finally eye gaze – in this smaller subset of VPs were analyzed initially and separately (*results*: section 2) from the VPs that contained AR sequences. The aim of this separate analysis was to generate a structure of these particular VPs for comparison with interactions that contained higher frequencies of ARs between partners to determine the similarities and differences in attention cues use in interactions with variable amounts of attention changes.

VPs that contained ARs were then subsequently analyzed (*results*: section 3) and included analyses of the orientation of each attention cue – body orientation first, then head orientation, and finally eye gaze. Data for all instances of attention (VPs with ATs or ARs) were then combined to analyze the congruency between eye gaze and head

orientation and then head orientation and body orientation *(results*: section 4). Finally, I evaluated the dyadic attention orientations at the end of interactions (in both VPs and controls) in relationship to the end interaction outcome (*results*: section 5). In the case of VPs, this interaction outcome was either the resumption of play or termination of the play bout.

Results

1. Initial analyses

Over the course of data collection, 87 play bouts[12] were recorded between gorillas with a mean duration of 166.7 seconds (bouts ranged from 11 to 685 s). These play bouts consisted of two distinct periods of lesser durations: play periods and vigilance periods (VPs). Each play bout contained a mean of 4.1 play periods lasting a mean of 22.0 s (n = 479, SD = 20.0 s, frequency range = 1-17 play periods) and a mean of 3.4 VPs lasting a mean of 14.8 s (n = 301, SD = 17.0 s, frequency range = 0-17 VPs).

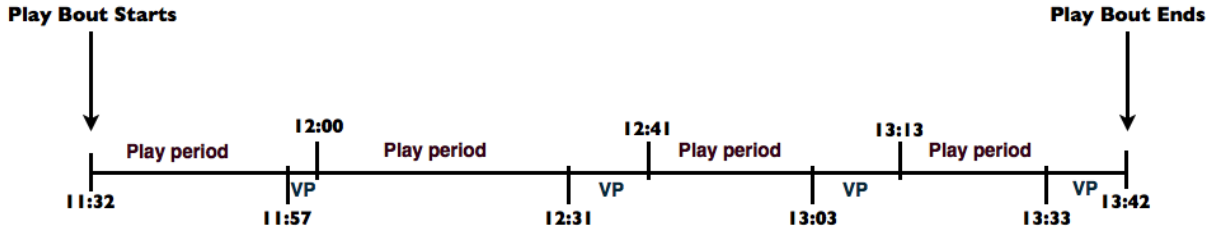


Fig. 27 – A timeline of an entire play bout and its composition of play periods and vigilance periods. This particular example contains 4 VPs and 4 play periods within the 130 second play bout. The frequency range for all play periods observed was 1-17 and the range for VPs was 0-17.

This study analyzed 63 non-play restful controls and 301 VPs (93 VPs were excluded

[12] A *play bout* was an entire playful interaction from the time of play initiation until the interaction termination and encompassed both play and VP time periods.

from further VP analyses because the entire length of the VP was not visible to the observer). The mean duration of controls was longer (M = 95.1 s; SD = 14.4 s) than the mean duration of VPs (M = 14.8 s; SD = 17.0 s). Controls spanned a time range from 7 to 590 s, whereas VPs spanned a shorter duration range from 2 to 136 s. A play period followed a VP the majority of the time (90.4%); however, an increase in the duration of a VP was not a predictor of play resumption (Logistic regression: $Wald$ = .619, p = .431).

The majority of VP scenarios (84.0%) contained gorillas that participated in a sequence of attention realignments (ARs), first orienting their attention away from their partner and then reorienting back toward their partner. The frequency of ARs was variable (ranged from 1-30) and an AR occurred either once or more during the progression of the interaction. The remainder of VPs (16.0%; n = 48 VPs) contained 0-1 AT (i.e., from an away orientation back toward the partner or from an orientation toward the partner to elsewhere within the environment) from the beginning of the VP to the end of the VP.

2. VPs with 0-1 AT

VPs with 0-1 AT were investigated initially; the mean length of these VPs was 7.0 s (SD = 5.7 s), and the majority of these VPs lasted ≤ 10 s (85.4%), which was shorter than the mean duration of interactions with ARs (see Section 3, pg. 157). Attention orientation was then further assessed for the three cues of body, head and eye gaze.

2.1. Body attention

The body orientations of the gorillas were similar at both the beginning and end of these VPs; at both time frames, the gorillas were more often oriented toward their partner

rather than away (*beginning* = 85.3%, *n* = 81; *end* = 87.3%, *n* = 83). Dyad body orientation also followed a similar pattern for both the beginning and end time frames in which a mutual orientation between partners was the most frequent (*beginning* = 76.6%, *n* = 36; *end* = 74.5%, *n* = 35). The remaining VPs (*n* = 12) contained one gorilla oriented toward their partner at the end of the VP (25.5%).

Body orientation was then compared for changes between the beginning and end time frames (Table 21). Typically, the gorillas did not alter their body orientation in relationship to their partner between the beginning and end points of the VP (91.6%, *n* = 87), and a torso directed toward the partner was the most common beginning and end orientation (82.1%). Three gorillas averted their body orientation from their partner at the end of the VP and five gorillas changed their body orientation toward their partner at the end of the VP; however, this pattern of change was not significant (*uncorrected McNemar test*: $\chi^2_{(1)} = 0.5$, $p = .48$).

	VP beginning	**VP end**	**%**	***n***
No change in body orientation	Toward	Toward	82.1%	78
	Averted	Averted	9.5%	9
Change in body orientation	Toward	Averted	3.1%	3
	Averted	Toward	5.3%	5

Table 21 – Beginning and end body orientations for vigilance periods with 0-1 attention transition (AT). Most often, no change in body orientation was observed between the beginning and end time frames of the VP, and a body directed toward a partner was the most occupied orientation.

2.2. Head attention

Head attention at the beginning of these VPs was comparable between orientations toward the partner (51.6%) and averted away (48.4%). The head attention of the dyad at the beginning of these VPs was comparable between all three orientations (*mutual* = 31.8%, n = 14; *one partner oriented* = 38.6%, n = 17; *neither partner oriented* = 29.5%, n = 13). At the end of VPs, a head oriented toward the partner was more frequently observed (73.4%, n = 69), and a mutual head orientation between dyad members was most often observed (50.0%, n = 22; *one partner oriented* = 38.6%, n = 17; *neither partner oriented* = 11.4%, n = 5).

Similar to body orientation analyses, the head orientations were compared for the beginning and end of VPs (Table 22). The gorillas were observed to remain with the same beginning and end orientation 61.9% (n = 57) of the time (*oriented toward the partner* = 70.2%, *oriented away* = 29.8%). A significant pattern of change was observed for an averted orientation; more gorillas were averted from their partner at the beginning of the interaction than at the end (*uncorrected McNemar test*: $\chi^2_{(1)} = 10.3$, $p = .001$).

	VP beginning	VP end	%	*n*
No change in head orientation	Toward	Toward	43.5%	40
	Averted	Averted	18.5%	17
Change in head orientation	Toward	Averted	8.7%	8
	Averted	Toward	29.3%	27

Table 22 - Beginning and ending head orientation frequencies for vigilance periods with 0-1 attention transitions. A toward orientation at both the beginning and the end of the VP was the most frequently observed head orientation (43.5%).

2.3. Eye gaze

Eye gaze was visible for each gorilla at the beginning of 47.9% of these VPs (n = 23) and was most frequently averted (87.0%). Eye gaze for the gorilla dyads at this time frame could only be observed in 10.4% of VPs (n = 5) and was averted (for both gorillas) in all instances. Eye gaze could only be evaluated for each gorilla in 16.7% of VPs (n = 16) and was most frequently averted from the partner (75.0%). Eye gaze could not be evaluated for both gorilla partners simultaneously at the end of VPs for this subset of cases.

Changes in eye gaze from the beginning to the end of the VP were only observable in 25.0% of VPs (n = 12). In the majority of these VPs (66.7%), the gorillas remained with an averted eye gaze at both time frames and there was no significant pattern of change observed (*uncorrected McNemar test*: $\chi^2_{(1)} = 0.3$, $p = .6$) [Table 23].

	VP beginning	VP end	%	*n*
No change in eye gaze	Toward	Toward	8.3%	1
	Averted	Averted	66.7%	8
Change in eye gaze	Toward	Averted	8.3%	1
	Averted	Toward	16.7%	2

Table 23 – Beginning and end eye gaze direction for vigilance periods with 0-1 attention transitions. Gorillas typically did not change their gaze direction between the two time frames and an averted gaze from the partner was the most frequent gaze orientation maintained (66.7%).

2.4. Summary

During this subset of VPs, gorillas typically maintained a mutual body attention toward one another. Head attention at the beginning was comparable between toward and away

orientations but became significantly directed toward the partner at the end of the interaction. When eye gaze was visible, it was averted and remained averted between partners.

3. VPs containing ARs

ARs were observed in the majority of both controls (87.3%, $n = 55$) and VPs (84.0%, $n = 252$). VPs had higher frequencies of low amounts of ARs per VP (e.g., 1, 2, or 3 realignments; Fig. 28). A significant difference was observed between the number of ARs present in controls and VPs (*VPs*: $M = 3.4$, $SD = 3.9$, $n = 301$; *controls*: $M = 7.3$, $SD = 8.5$, $n = 63$; *Wilcoxon signed-rank test*: $Z = -3.5$, $p = .001$).

The higher mean number of ARs and the longer mean durations observed in controls ($M = 7.3$, *duration* = 95.1 s) compared to VPs ($M = 3.4$, *duration* = 14.8 s) led to an evaluation of the relationship between the duration of the VP and number of ARs between gorilla partners. For controls, a significant positive correlation was observed between the two variables (*Spearman's rho:* $r = .528$, $n = 63$, $p < .001$), which indicated that the number of ARs between gorilla partners typically increased as the duration of the control increased (Fig. 29). A significant positive correlation was also observed between the VP duration and number of ARs ($r = .649$, $n = 301$, $p < .001$). These results also indicated that the number of ARs between gorilla partners typically increased as the duration of the VP increased.

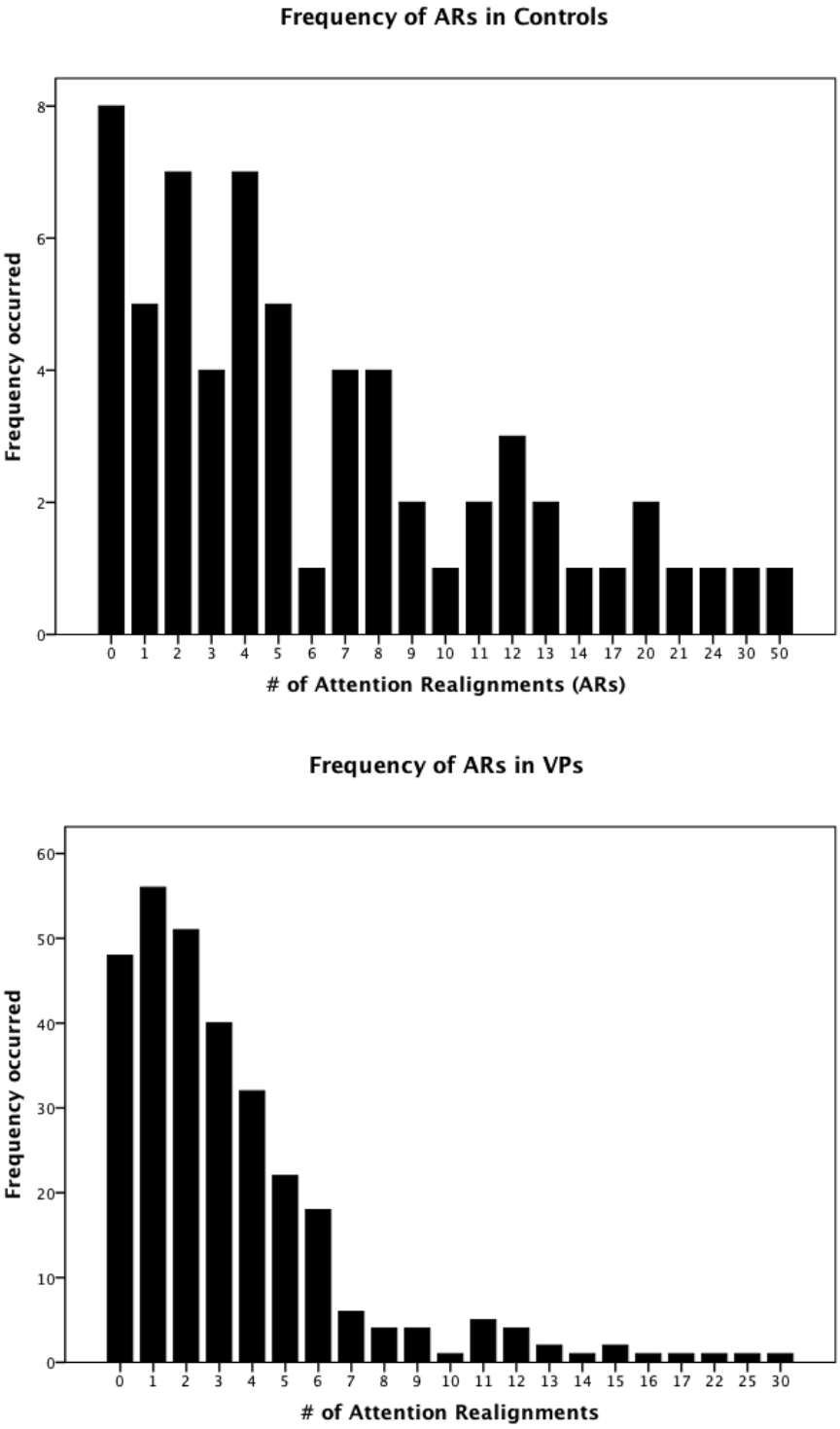


Fig. 28 – The frequencies of attention realignments (ARs) observed during controls and vigilance periods. VPs had repeated occurrences of lower amounts of ARs compared to controls; controls had a higher maximum amount of ARs (50) compared to VPs (30).

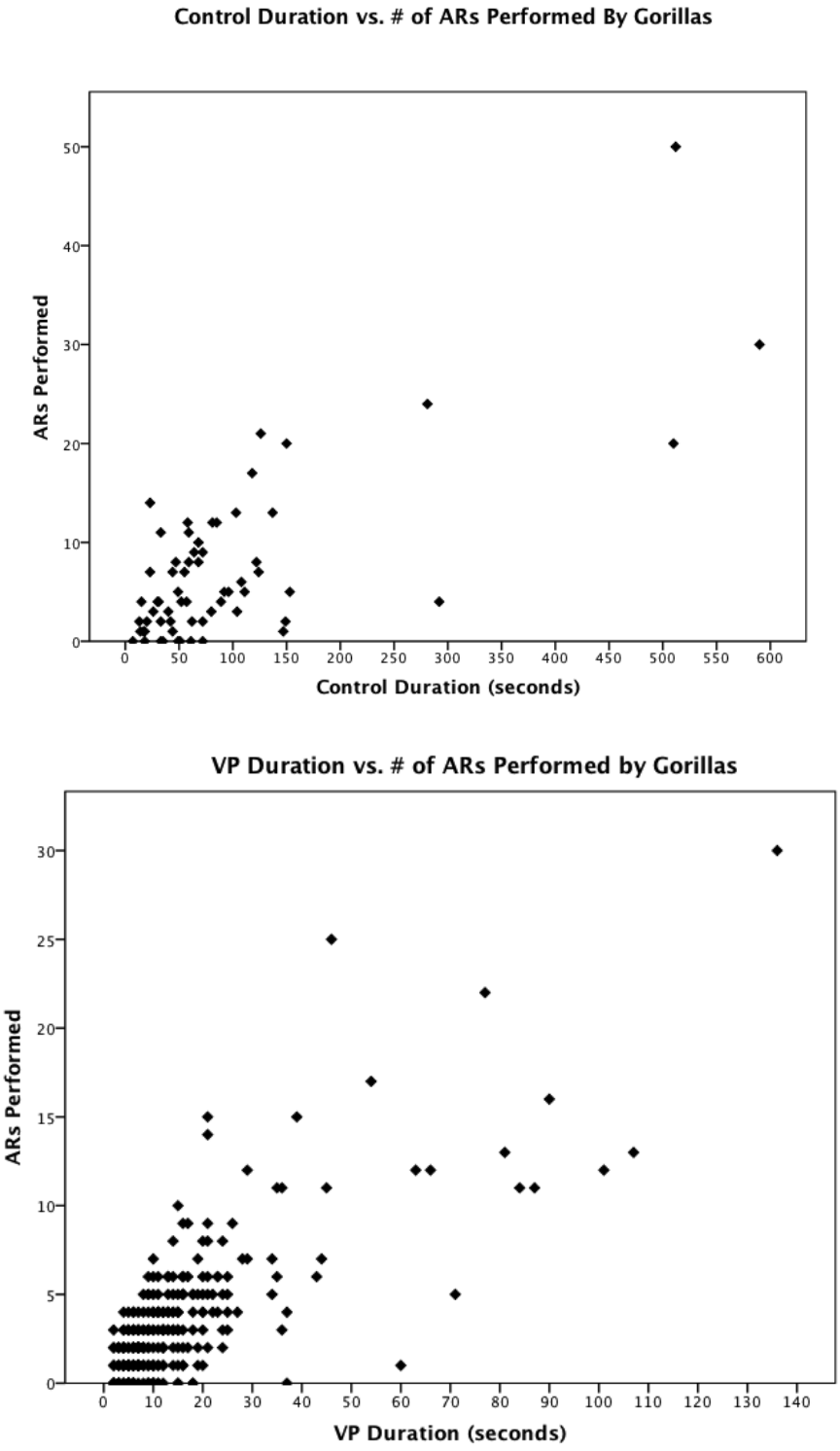


Fig. 29 – Significant positive relationships were observed between the interaction duration (in seconds) and number of attention realignments (ARs) in controls (**top**) and vigilance periods (**bottom**).

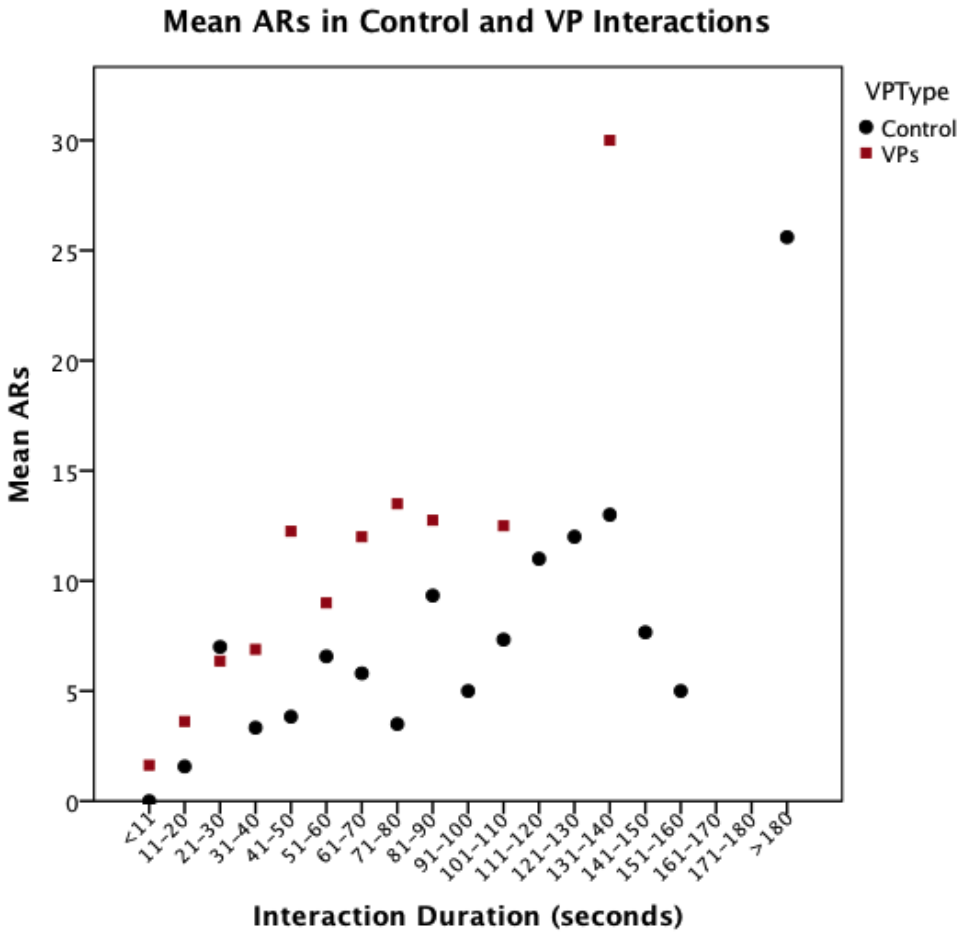


Fig. 30 – The mean number of attention realignments (ARs) per duration interval (in seconds) for controls and vigilance periods. This graph illustrates a higher density of ARs occurring during VPs in comparison to control interactions. All VP durations observed were less than 150 seconds with a mean duration of 14.8 seconds. The majority of VPs in which ARs occurred (96.0%, $n = 289$) lasted less than 60 seconds.

The interaction durations could be further categorized into spans of time (< 11 s, 11-20 s, 21-30 s, etc.), and it was observed that although VPs had a shorter mean duration than controls, ARs typically occurred in higher frequency (Fig. 30). In sum, although there was a general relationship between the interaction length and number of ARs, VPs between active play periods presented a significantly higher density of ARs than restful controls.

3.1. Body Attention

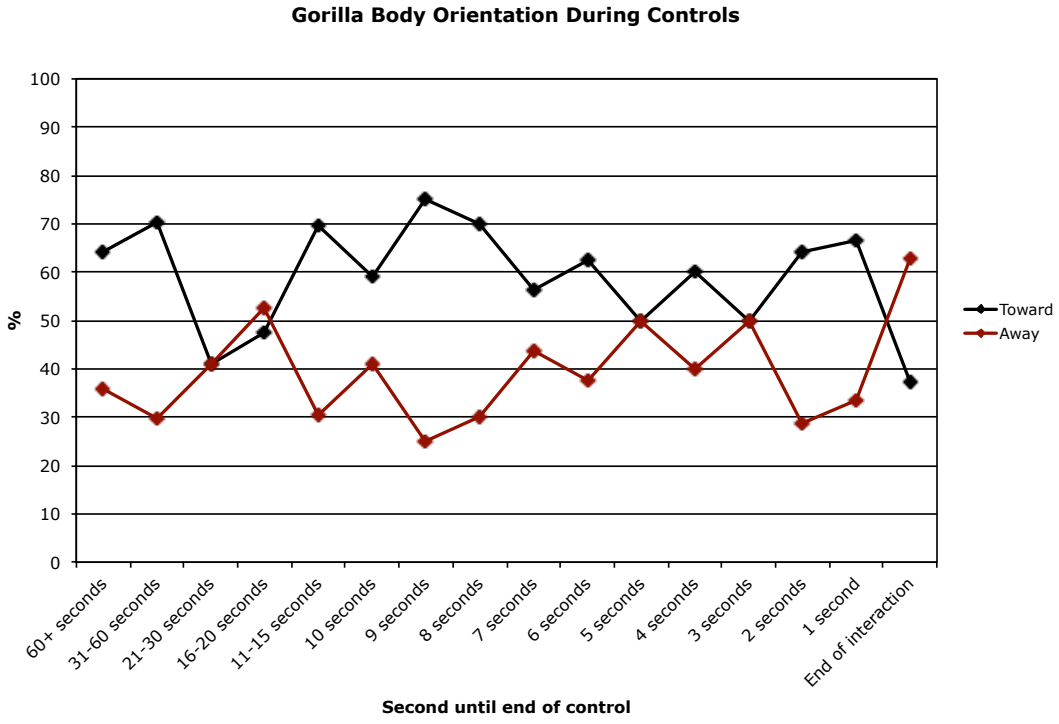
The measure of body attention was again determined by the direction of the gorilla's torso. At the beginning of VPs, the gorillas most frequently had their body oriented toward their partner (81.8%), and a mutual orientation between both gorillas was the most observed dyad orientation (68.4%, $n = 201$; *one partner oriented* = 26.5%, $n = 78$; *neither partner oriented* = 5.1%, $n = 15$).

A Friedman's test showed a statistically significant difference in the frequency of a toward orientation by time frame until the end of the control interaction ($\chi^2_{(15)} = 75.9$, $p < .001$). A post-hoc analysis with Wilcoxon Signed-Rank tests was conducted with a Bonferroni correction applied and a significance level set at $p < .003$. Successive time frames were compared (e.g., 9 to 8 s, 4 to 3 s, etc.) to determine whether the frequency of a toward orientation differed as the interaction approached termination; however, no significant stepwise comparisons were observed ($p > .003$; Fig. 31, top).

A Friedman's test showed a statistically significant difference in the frequency of a toward orientation by time frame until the end of the VP interaction ($\chi^2_{(15)} = 42.1$, $p < .001$). A post-hoc analysis with Wilcoxon Signed-Rank tests was conducted with a Bonferroni correction and a significance level set at $p < .003$. Successive time frames were compared to determine whether the frequency of a toward orientation differed as the interaction approached termination. No significant stepwise comparisons were observed ($p > .003$). However, a body orientation toward a partner was observed > 60% of the

time throughout VPs, and this frequency increased to > 80% as the VP approached termination (Fig. 31, bottom).

At the end of VPs, body orientation remained frequently oriented toward the partner (81.7%, *n* = 410), and the dyad most frequently occupied a mutual body orientation (67.1%, *n* = 167; *one partner oriented* = 28.9%, *n* = 72; *neither partner oriented* = 4.0%, *n* = 10). Control gorillas were more frequently oriented away from their partner at the end of an interaction (62.7%, *n* = 69), and the gorilla dyad was most often one partner oriented away (60.0%, *n* = 33; *neither partner oriented* = 32.7%, *n* = 18; *mutual orientation* = 7.3%, *n* = 4).



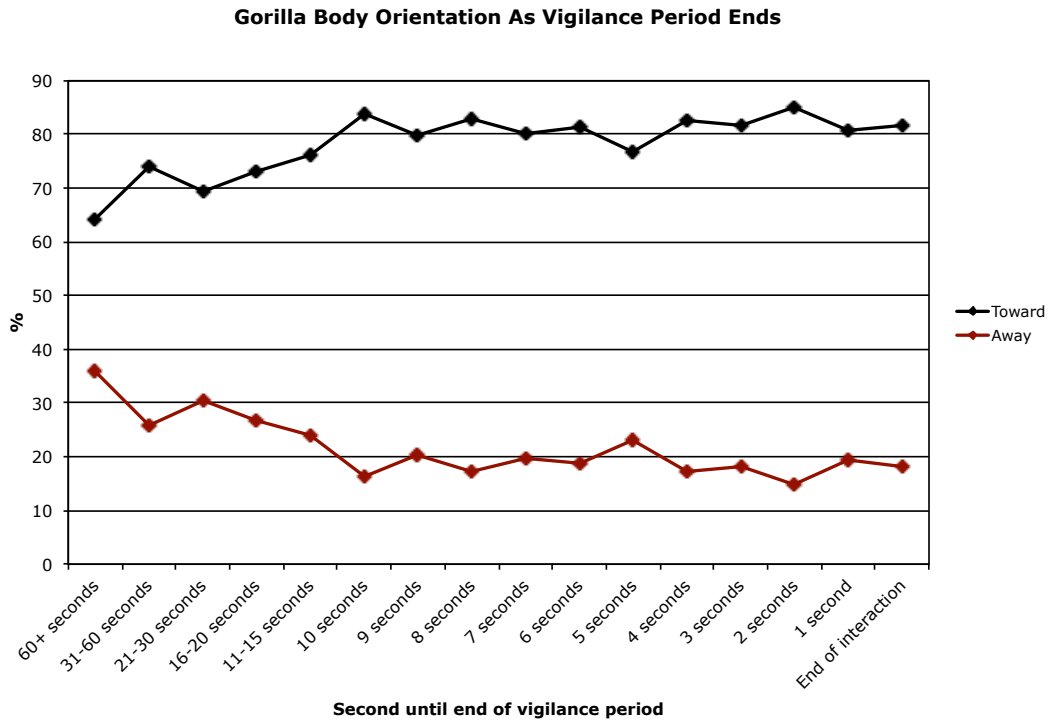


Fig. 31 – Control (**top**) and vigilance period (**bottom**) graphs of overall gorilla body orientation frequencies; the x-axis displays the length of time until the end of the interaction. Throughout VPs, gorillas had their body oriented toward their partner greater than 60% of the time, and this orientation frequency increased as the VP progressed from the beginning to the end.

3.2. Head Orientation

At the beginning of VPs, head orientation was comparable between toward and away orientations (*toward* = 47.2%, *n* = 231; *away* = 52.8%, *n* = 258), and the gorilla dyad was most frequently only one gorilla oriented toward the partner (47.5%, *n* = 112; *neither partner oriented* = 28.4%, *n* = 67; *mutual orientation* = 24.1%, *n* = 57).

Head orientation was assessed throughout each control and VP when the gorillas performed an AR. During control interactions, a Friedman's test showed a statistically significant difference in the frequency of a toward orientation by time frame until the end

of the control interaction ($\chi^2_{(15)} = 77.5$, $p < .001$). A post-hoc analysis with Wilcoxon Signed-Rank tests was conducted with a Bonferroni correction applied and a significance level set at $p < .003$. Successive time frames were compared (e.g., 9 to 8 s, 4 to 3 s, etc.) to determine whether the frequency of a toward orientation differed as the interaction approached termination. No significant stepwise comparisons were observed ($p > .003$).

Head orientation was compared in the same manner for VPs. A Friedman's test showed a statistically significant difference in the frequency of a toward orientation by time frame until the end of the VP interaction ($\chi^2_{(15)} = 40.4$, $p < .001$). A post-hoc analysis with Wilcoxon Signed-Rank tests was conducted with a Bonferroni correction and a significance level set at $p < .003$. Successive time frames were compared to determine whether the frequency of a toward orientation differed as the interaction approached termination. No significant stepwise comparisons were observed ($p > .003$). However, a head orientation toward a partner was observed > 55% of the time throughout VPs, and this frequency increased as much as 72% as the VP progressed to termination (Fig. 32).

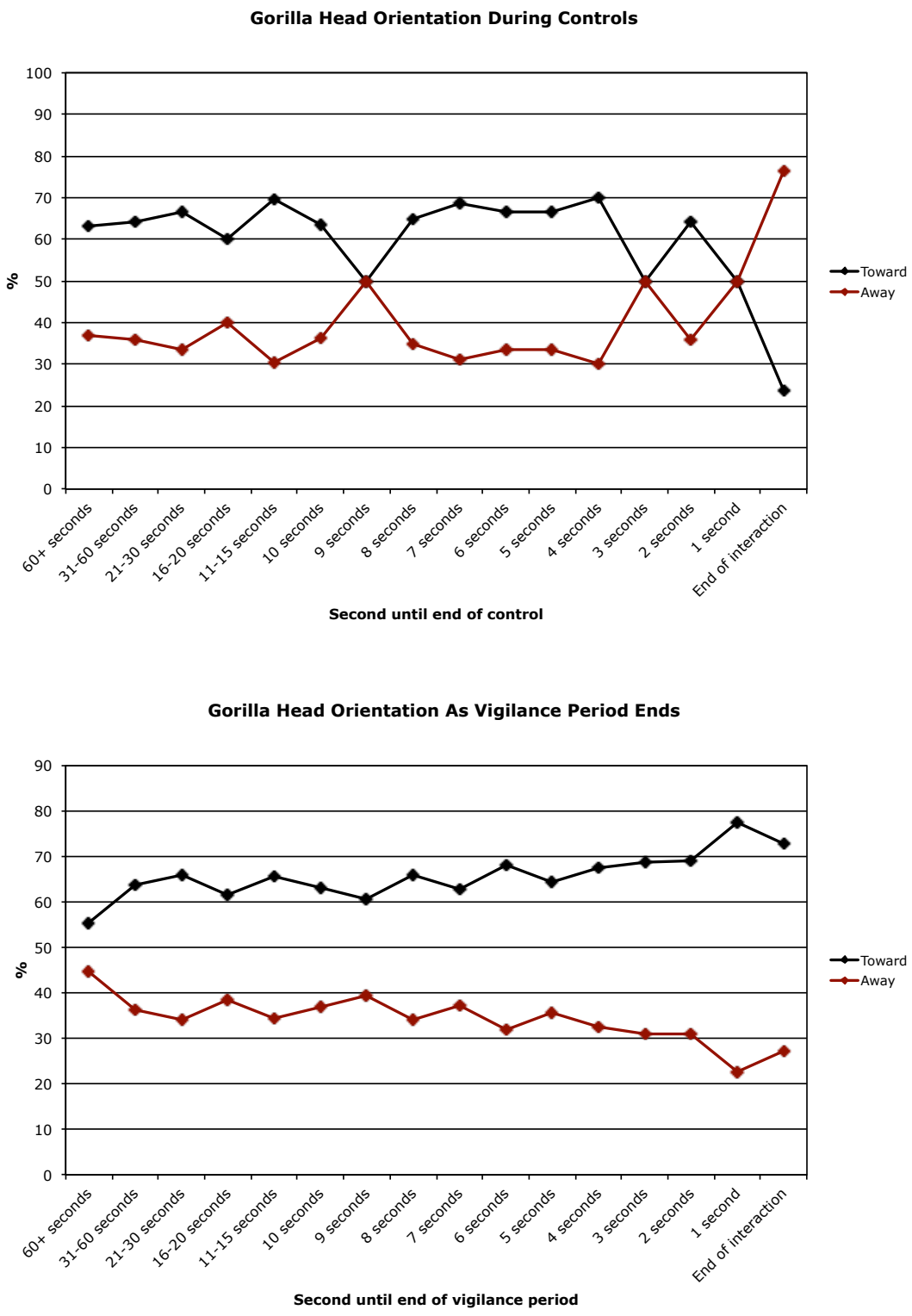


Fig. 32 – Graph of head orientation during controls and vigilance periods. Head orientation overall during VPs was most frequently directed toward a partner and this frequency increased as the VP drew to an end.

At the end of controls, gorillas were more frequently oriented away from their partner (73.6%, *n* = 81), and the gorilla dyad was most often neither partner oriented (60.0%, *n* = 33; *one partner oriented* = 32.7%, *n* = 18; *mutual orientation* = 7.3%, *n* = 4). At the end of VPs, head orientation remained frequently oriented toward the partner (72.8%, *n* = 358), and the dyad most frequently occupied a mutual body orientation (51.9%, *n* = 124; *one partner oriented* = 41.4%, *n* = 99; *neither partner oriented* = 6.7%, *n* = 16).

3.3. Eye gaze

Data collection for eye gaze in VPs was difficult to assess in a majority of the data subset because of 1) the physical restrictions of the exhibit, which increased the distance between the gorillas and observer's video camera; 2) the limitations imposed by the proximity of the gorillas to one another. If the gorillas were sitting far apart from one another, then the camera had to zoom out to incorporate both partners within the same frame; and 3) the dark nature of gorilla faces and eyes. At the beginning of VPs, eye gaze was most frequently directed away from the partner (85.0%, *n* = 140), and neither gorilla oriented was the most frequent dyad orientation (67.9%, *n* = 19; *one partner oriented* = 21.4%, *n* = 6; *mutual orientation* = 10.7%, *n* = 3).

Eye gaze was assessed throughout each control and VP when the gorillas performed an AR. There were insufficient cases for each gorilla for a statistical analysis of orientation during controls; however, control gorilla eye gaze was most frequently oriented away throughout interactions (83.3%, *n* = 140) [Fig. 33, top].

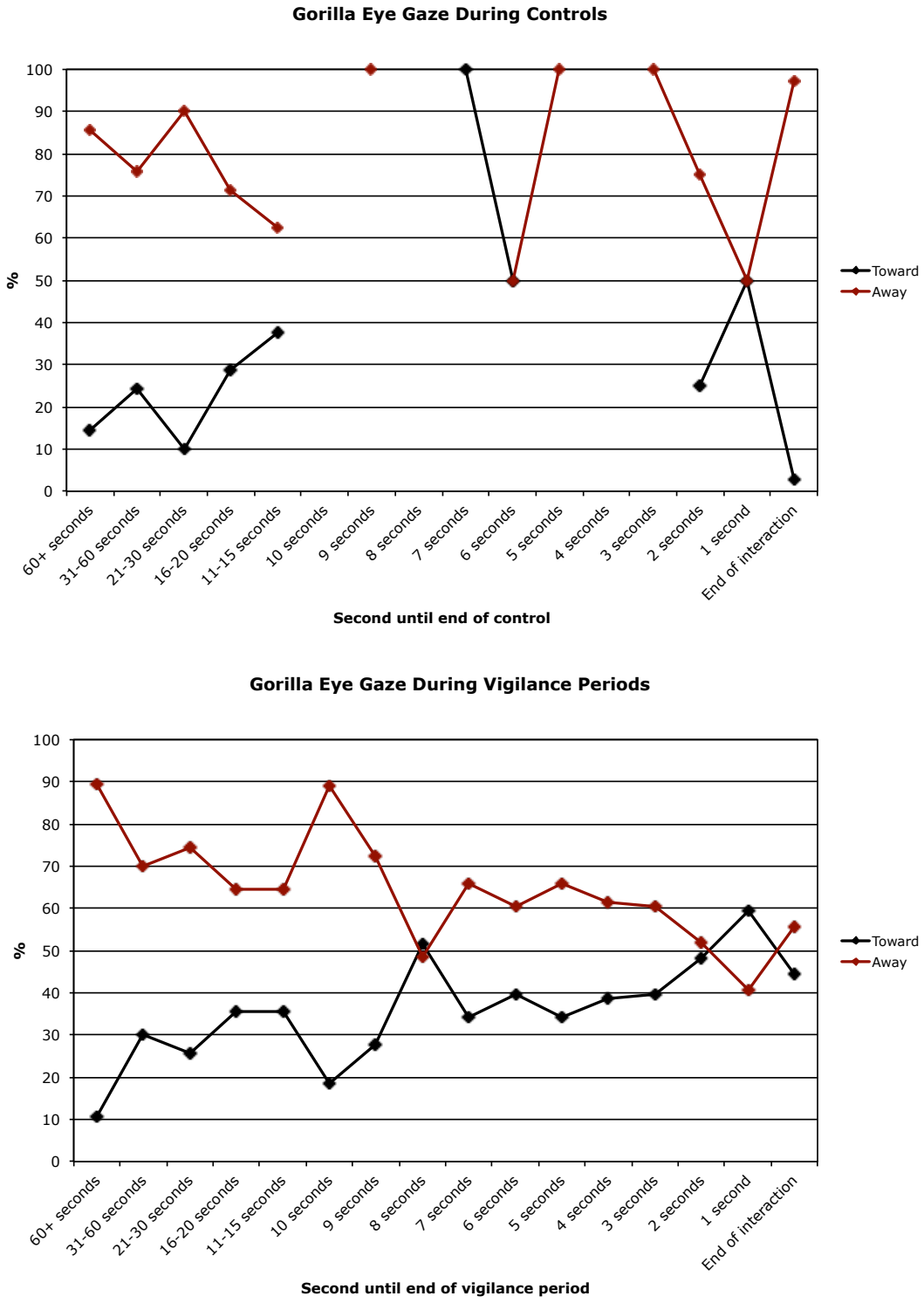


Fig. 33 – A graph of eye gaze changes in relationship to their partner throughout controls and vigilance periods. Over the course of the last 5 seconds of VPs, eye gaze became more frequently directed toward the partner.

During VPs, a Friedman's test showed a statistically significant difference in the frequency of a toward orientation by time frame until the end of the VP interaction ($\chi^2_{(15)} = 32.1$, $p < .006$). A post-hoc analysis with Wilcoxon Signed-Rank tests was conducted with a Bonferroni correction and a significance level set at $p < .003$. Successive time frames were compared to determine whether the frequency of a toward orientation differed as the interaction approached termination. No significant stepwise comparisons were observed ($p > .003$); however, VPs showed a decline in the frequency of averted eye gaze as the VP approached termination (Fig. 33, bottom).

At the end of VPs, eye gaze was comparable between toward (44.4%, n = 52) and averted orientations (55.6%, $n = 65$). Dyad eye gaze was also nearly equally distributed for the three attention categories (*one partner oriented* = 36.8%, $n = 7$; *neither partner oriented* = 31.6%, $n = 6$; *mutual orientation* = 31.6%, $n = 6$)

3.4. Summary

In general, individual gorilla and dyad body attention were significantly oriented toward and in mutual orientation throughout the majority of VP interactions. Individual gorilla head orientation was comparable between toward and away orientations at the beginning of VPs but became significantly oriented toward the partner at the end of the VP. Both individual and dyad gorilla eye gaze orientations were significantly averted away from the partner at the beginning of VPs but were comparable between toward and away orientations at the end of VPs (Fig. 33).

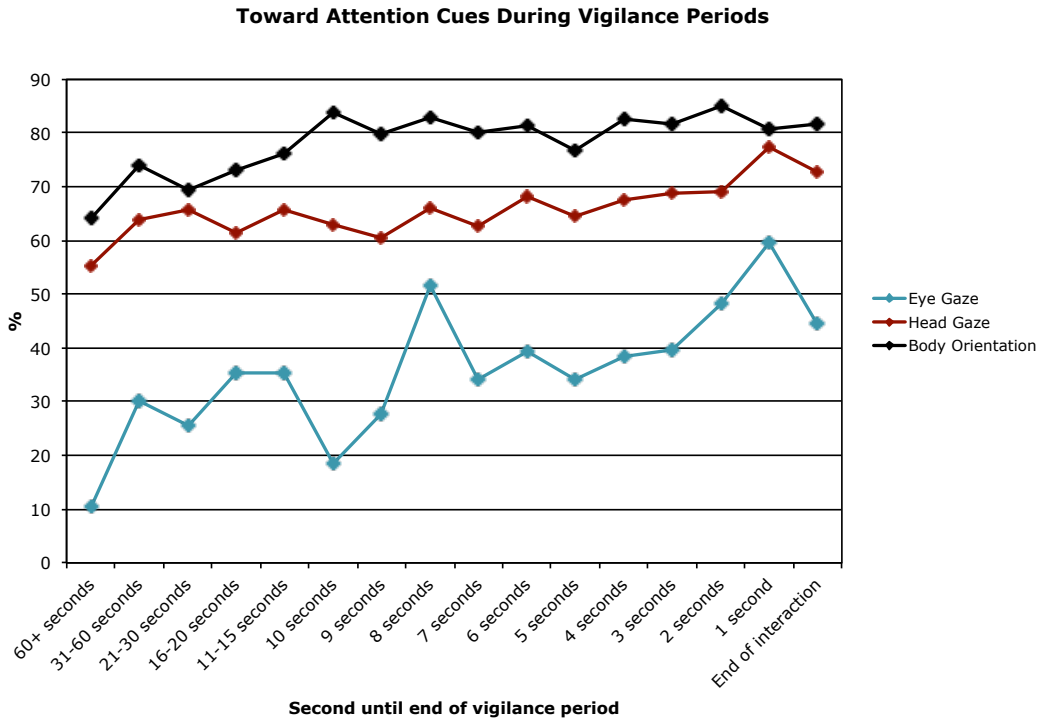


Fig. 34 – The combined toward attention cues (toward body, head, and eye gaze) throughout vigilance periods.

4. Attention cue congruency

Data for the three attention cues were paired for examination – eye gaze with head orientation and body orientation with head orientation – for all exchanges of attention during VPs and controls. This analysis was performed to determine the congruency between attentional cues used by the gorillas. If both cues were oriented in the same direction they were deemed congruent, regardless of whether they were directed at the partner or not. For example, was the direction of eye gaze also the direction of head orientation?

4.1. Eye gaze and head orientation congruency

Gorillas showed high levels of eye gaze and head orientation congruency in both controls (92.4%, n = 145) and VPs (93.6%, n = 701). A comparison of control and VP congruency levels showed no significant difference between the frequencies in each interaction type (*Wilcoxon signed-rank test*: z = -1.5, p = .14), which indicated that congruency occurred in both types of interactions in similar amounts.

4.2. Head and body orientation congruency

Gorillas showed high levels of head and body orientation congruency (i.e., the head and torso were aligned in the same direction) in controls (67.8%, n = 769) and VPs (74.9%, n = 2246). A comparison of control and VP congruency levels showed no significant difference between the frequencies in each interaction type (*Wilcoxon signed-rank test*: z = -1.5, p = .14), which indicated that congruency occurred in both interaction types in similar amounts.

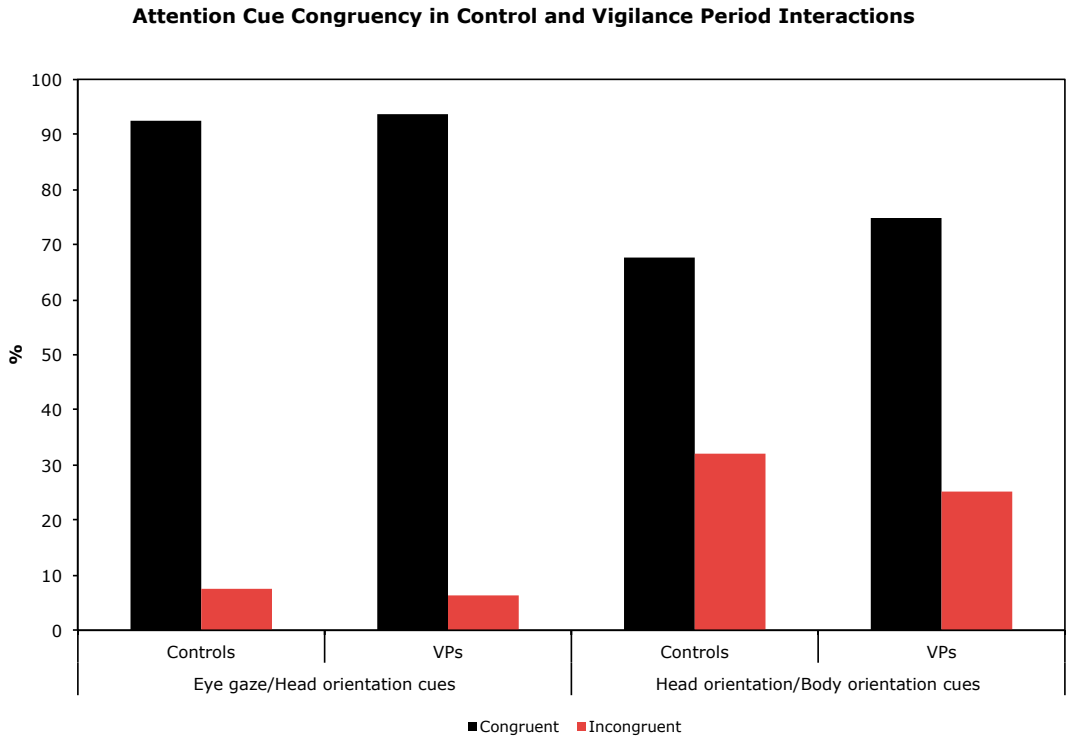


Fig. 35 – Graph of attention cue congruencies, eye gaze with head orientation and head orientation with body orientation, in controls and vigilance periods. Overall, pairs of cues were more frequently congruent than incongruent in both interaction types.

4.3. Summary

In general, there was high cue congruency between eye gaze and head orientation and between head and body orientations throughout both controls and VPs. No significant differences were observed between the congruency frequencies for either interaction type, which indicated that cue congruency was used similarly in both types.

5. Interaction outcome

The orientations of attention cues at the end of a VP were further examined to determine the relationship between the final orientations of these cues and the end interaction results. The end result after a VP was either a resumption of play or a termination of the

interaction between the gorillas. VPs with both ATs and ARs were combined for analysis, and play was observed to resume at the end of 90% of VPs (n = 271) whereas the remaining interactions terminated (10%, n = 30). The number of changes in an attention cue (AT or AR) during a VP was observed to be a predictor of a play period occurring after a VP (*Logistic regression*: $EXP\beta = 1.1$, *Wald* = 9.1, $p = .002$), i.e., when the number of changes in an attention cue increases by 1, play is 1.1 times more likely to occur following the VP. The end orientation for each attention cue of the gorilla dyad was then analyzed to examine whether particular orientations corresponded with the resumption or termination of play.

5.1. Body attention

Play resumption occurred most frequently when the gorilla dyad had a mutual body orientation (74.1%, n = 198) and least frequently when neither gorilla had their body oriented toward the other (0.4%, n = 1). When the interaction terminated, most often only one gorilla of the dyad was attending with their body (55.2%, n = 16) [Table 24].

	Play resumes	***n***	**Interaction terminates**	***n***
Neither gorilla oriented	0.4%	1	31.0%	9
One gorilla oriented	25.5%	28	55.2%	16
Both gorillas oriented	74.1%	198	13.8%	4

Table 24 – Dyad body orientations at the end of VPs and the frequencies of play resumptions and interaction terminations.

5.2. Head attention

When play was resumed, the end head orientation of the gorilla dyad was most frequently a mutual head orientation (56.6%, n =146) [Table 25]. Interestingly, when interaction termination occurred, the dyad most frequently had only one gorilla attending to their

partner (63.0%, *n* = 15).

	Play resumes	*n*	Interaction terminates	*n*
Neither gorilla oriented	5.0%	13	29.6%	8
One gorilla oriented	38.4%	99	55.6%	15
Both gorillas oriented	56.6%	146	14.8%	4

Table 25 – Dyad head orientations at the end of VPs, and the frequencies of play resumptions and interaction terminations.

5.3. Eye gaze

Eye gaze data for both gorilla partners at the end of VPs was only measurable in a small sample of cases (*n* = 19, 6.3% of total VPs) because of enclosure and observer constraints; therefore, any conclusions from the current results need further verification with larger sample sizes. When the gorillas resumed play, eye gaze of the gorilla dyad was most frequently mutual attention (40.0%, *n* = 6) although one gorilla gazing and neither gorilla gazing were common orientations (*one gorilla* = 33.3%, *n* = 5; *neither gorilla* = 26.7%, *n* = 4). Eye gaze when the interaction terminated was equally divided for one gorilla gazing (50.0%, *n* = 1) or neither gorilla gazing (50.0%, *n* = 1) [Table 26].

	Play resumes	*n*	Interaction terminates	*n*
Neither gorilla oriented	26.7%	4	50.0%	1
One gorilla oriented	33.3%	5	50.0%	1
Both gorillas oriented	40.0%	6	0%	-

Table 26 – Dyad eye gaze orientations at the end of VPs and the frequencies of play resumption and interaction termination.

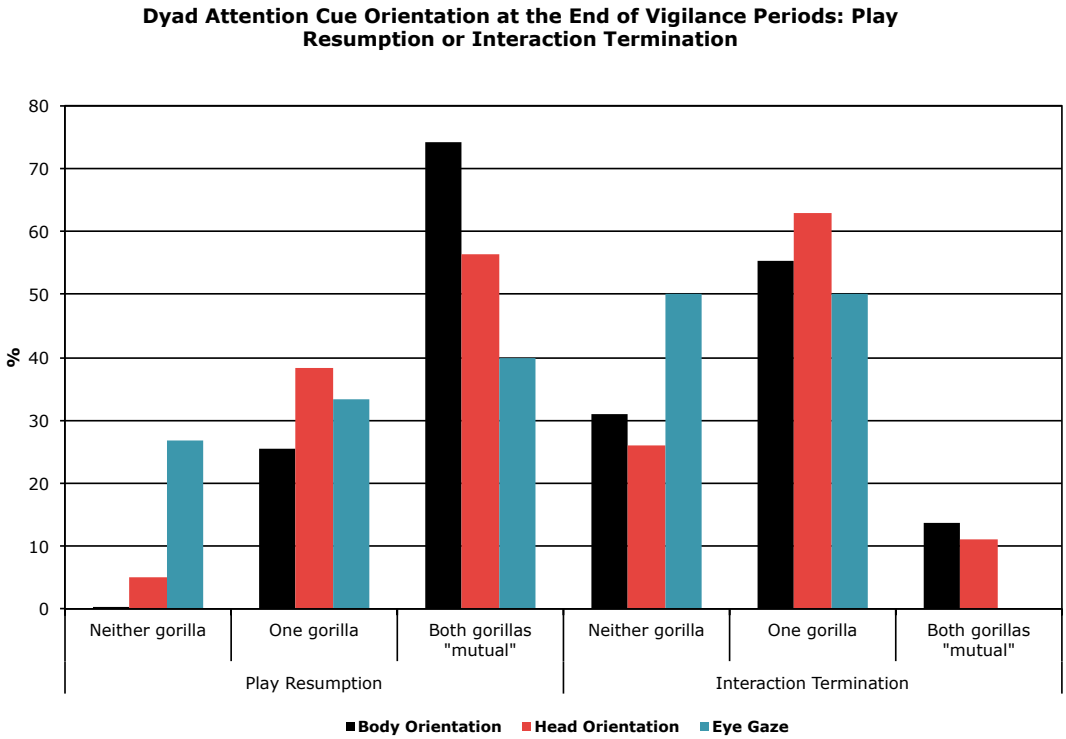


Fig. 36 – Distribution of dyad attention orientations for body, head, and eye gaze cues at the end of vigilance periods (VPs). When play was resumed at the end of a VP, body orientation, head orientation, and eye gaze were most often in mutual orientation between partners.

Discussion

This study was an exploration of attention cues throughout two contextually different types of interaction to investigate how attention cues were displayed and used by and between gorilla play partners. The initial analysis of VPs revealed that the majority contained one or more changes in attention.

ARs between gorillas were observed in higher densities in VPs than in controls. ARs of VPs were frequent within shorter interaction durations, which suggests that attention may be used differently in VPs than in non-playful rest control situations. The realignment of attentional cues to attain an orientation directed toward a partner may be more socially

beneficial in a VP scenario than during a non-VP. One potential reason for this may be based simply on the overall context of VPs. VPs occur after an involvement in a play period and/or between play periods, which naturally places this interaction type in a different behavioral context than the non-playful rest context of controls.

Greatly differing from periods of rest, play is a highly active exercise, which engages the gorillas behaviorally, physically, and socially. It would therefore be expected that in the interim period of time between play periods, in which the physical and overt behavioral nature of the play context is temporarily suspended, the gorillas would remain engaged on a social level to anticipate or prepare for the resumption of physical play behaviors. This social engagement is expressed and assessed through attentional behaviors involving the combination of body, head, and eye gaze cues. During VPs, gorillas produce frequent ARs where the alignment of an attentional cue toward the partner not only works to inform about attention direction but also might communicate more complex information about the receptiveness and potential future actions of the partner. In this manner, attention could be used in two potential capacities, both gathering and communicating information, which would be advantageous for both the realigning gorilla and their partner. The realigning gorilla would gain useful information about the state of their partner through the monitoring of the partner's activity and actions. A sustained realignment, where a gorilla remains oriented toward their partner, could also potentially indicate participation or readiness for further social interaction. For example, a partner-directed head orientation that remains partner-directed for the majority of the interaction might indicate to the partner a receptiveness to resume play. The receiving gorilla would

also gather information from the realignment about the partner's direction of attention and potential participation in a subsequent interaction.

Attentional changes between partners occurred on all three attention levels throughout both VPs and controls. The broadest measure of attention, body orientation, showed different general trends between the interaction types. Controls alternated between toward and away orientations throughout the interaction, whereas VPs showed a body orientation that was consistently oriented toward their partner. This difference in body orientation between controls and VPs indicates that within VPs, gorillas may use the positioning of their body differently than during controls. The orientation of the torso, which is a broad and easily visible directional indicator, can quickly inform other gorillas about the probable attention or action direction of a partner. Further to being a possible cue of attention direction, a torso that is directed toward a partner has the potential to be a cue that not only indicates a basic level of attentiveness, but a cue of receptiveness to interaction and direction of attention. Sensitivity to a front or back body orientation has been shown in bonobos, chimpanzees, and orangutans that made food requests from a human experimenter (Hostetter & Alibali, 2007; Kaminski *et al*., 2004).

Because VPs follow play periods, body attention would be an essential social cue for a gorilla to utilize to indicate a continued participation. Therefore, the maintenance of such a cue toward a partner would allow the gorilla to retain an impression of receptivity to that partner. This would be beneficial for a play partner to recognize, especially if the true attention of the receptive gorilla (i.e., eye gaze) is directed elsewhere temporarily

within the environment. This would also prove advantageous for the receptive gorilla, since their true attention (deployed through eye orientation) would be free to evaluate the surrounding environment, meanwhile, indicating participation to their play partner. Since a distinctive feature of play behavior is reciprocity between the interacting partners, having the means to quickly establish a partner's willingness or likelihood to participate would be valuable for successfully reengaging in a play period.

Head orientation is also a large and easily visible cue for judging direction of attention. Again, the orientation trends differed between controls and VPs, which suggests a difference in its use between the two interaction types. Similar to the results for VP body orientation, head orientation was a cue that was consistently oriented toward the partner throughout VPs. Since the face also contains the eyes, head orientation is an attentional cue that has the capacity to work on dual levels. The high level of congruency between head and eye gaze cues observed in this study suggests that where a gorilla head was directed was also typically where eye gaze was directed. Therefore, aligning the head toward the partner may actually be an indication that the gorilla is monitoring the actions of the partner; the high frequency of toward orientations that were observed in VPs may signify a higher and more consistent amount of partner monitoring. Attention monitoring thus appears to be valuable for the VP context; the high frequency of a toward orientation coupled with high congruency between head and eye cues demonstrates that the head cue alone, typically conveys as much information as eye gaze. This should however be further validated with additional eye gaze studies, based on this study's low frequency of clearly visible eye gaze. The congruencies of these cues would be beneficial for gorillas

in terms of conveying gaze information or hastening gaze direction detection since, as discussed in Chapters 2 and 3, gorillas tend to have dark coloration of the facial skin, hair and eyes, which has the potential to make it difficult to detect the direction of gaze. As discussed in the previous chapters, it has been suggested that this dark coloration could be an adaptation to camouflage gaze direction; however, this study's result of high congruency between head and eye gaze does not support this hypothesis, as head direction would be a relatively reliable indication of attention direction. Attention monitoring would serve to gather information about the state of the partner, e.g., proximity, behaviors, direction of attention, etc., thus further emphasizing the information provided by body orientation cues and potentially influencing one's own behavioral state and the successful resumption of play. Additionally, as was suggested for body attention, orienting the head attention toward the partner may be a potent reflection of willing participation in an interaction, especially if coupled with an attending eye gaze. Despite the above, it is also noteworthy that all attentional signaling is not necessarily intentional; neither does this signaling need to be understood in mentalistic terms by the interacting participants.

The difference in eye gaze between controls and VPs also differed. In contrast to body and head orientations, VP eye gaze was more frequently oriented away from the partner throughout VPs but became directed toward the partner as the VP approached termination. This increase in an attending eye gaze coupled with a consistent attending head orientation denotes an increase in partner monitoring as the VP draws to an end. It is possible that during a VP, body orientation acts as a cue of availability or willingness

to continue with play at a later time, and an averted eye gaze acts as a type of "not right now" cue. As the VP progresses, eye gaze that is oriented toward the partner becomes a "now" reengagement cue.

However, these results for eye gaze should be taken with caution because of the small sample size. This small sample was mainly because of proximity restrictions to the gorillas based on the large size and layout of the exhibit, which lent to the overall difficulty of eye gaze detection in the dark eyes of the gorillas. This particular difficulty indirectly supports the results of Chapters 2 and 3 that a white sclera does confer some advantage to human observers for gaze direction detection, at least from a distance. Since eye gaze of this study was difficult to monitor based on certain data collection limitations, future work on VPs should focus on incorporating methodological revisions to assess eye gaze in a more specific and substantial evaluation. For example, a study with sole focus on examining the faces of gorillas, i.e., data sampling that concentrates only on the face of the dyad members during a VP would be productive for determining the true nature of eye gaze use in VP gorillas.

Previous studies on eye gaze among the great apes offer some contrasting views that challenge the eye gaze and head orientation congruency results observed in this study but generate some interesting topics for comparison and future exploration. An examination of three types of eye gaze – fixations, scans, and glances – in chimpanzees (Bethell *et al*., 2007) argues against congruency of head and eye gaze cues and indicates that eye gaze was often used independently and in a manner incongruent with the direction of the head.

Bethell *et al*. reported this incongruency for 12-21% of gaze fixations, 42-49% of enclosure scans, and during 70-100% of glances, i.e., different types of eye gaze had different amounts of eye and head congruency. One explanation for the difference between the results of Bethell *et al*. (2007) and this study is a species difference, as chimpanzees may use eye gaze differently in comparison to gorillas. A second possibility is a contextual difference; Bethell *et al*. (2007) evaluated these three gaze types only within the contexts of feeding, grooming, and resting, whereas this study focused on VPs in a play context. Even so, the restful controls of this study, where gorillas also rested, fed, and on occasion groomed one another, did not produce comparable results to the chimpanzees.

A second study suggests that gazing out of the side of the eye toward a conspecific is the preferred method of gazing in Bornean orangutans (*Pongo pygmaeus*), again arguing against head and eye gaze cue congruency (Kaplan & Rogers, 2002). The results of at least these two studies suggest that these two species of great apes might use distinctive techniques of eye gaze when interacting with conspecifics within the social environment. While the majority of the data in my study supported congruency between head and eye gaze, there were examples within the data set where the gorillas also exhibited sideways gazing and instances of head and eye gaze incongruency. It is possible that this study may not reflect the true nature of congruency between these two cues because of the small sample size of observable eye gaze. Alternatively, gorillas might possess an eye-head congruency pattern that differs from other apes, at least in the specific context of social play addressed in my study. Further research is essential to quantify the extent in

which cue congruency is a typical occurrence in gorillas.

Overall, the variable presence of ARs and a tendency to orient attention cues in a partner-directed manner during VPs indicates that these time frames, interspersed among active play, are socially complex and important for playing individuals. Ultimately, attention has two potential uses: 1) to monitor the actions and attention of the play partner; and 2) to convey to a partner social receptiveness and participation to impending interactions. Cue location, mobility, and size naturally impose limiting restrictions on the capacities of these attentional cues, and one cue may be better suited for one particular purpose over another. However, either taken in isolation or in combination, these attentional cues have the ability to regulate a social interaction through the conveyance of a great deal of socially relevant information that is not only useful for the immediate VP – cues that indicate "not right now" and "now" – but also in preparation for a subsequent interaction. The differences in the orientation trends observed between non-play restful controls and VPs suggest that in general, attention may be used differently in VPs than in other neutral type interactions. Until now, VPs have yet to be addressed as a component of the play literature, mainly because they have seemed like little more than transitory periods of rest between one play period and another. This study suggests that VPs are far from moments of social disengagement between partners and instead might, in fact, be an important part of play behavior because they may maximize the possibility for gorillas to learn about the social cognitive cues that regulate social interactions.

CHAPTER 5:

Gorilla postures and actions during changes in attention orientation in vigilance periods

Chapter 5: Gorilla postures and actions during changes in attention orientation in vigilance periods

Introduction

The preceding study, Chapter 4, was an examination of the social cues of attention in control and vigilance period (VP) interactions with a specific analytical focus on the distribution of attention orientations and the presence of "attention transitions" (ATs) and "attention realignments" (ARs) between gorilla partners. A VP contained an AR if a gorilla averted their attention (either eye, head, or body) from the partner and then in the ensuing progression of the interaction, realigned their attention back toward their partner. In instances where a gorilla did not participate in an AR, the interaction was categorized as participating in an AT, in which their attention "transitioned" either toward or away from their partner (if it transitioned at all). These broad groupings were also retained for Chapter 5 to maintain data and analysis consistency between the chapters.

This study complements the preceding attention orientation analyses of Chapter 4 by examining the gorilla postures and actions that accompanied the frequent changes in the attention cue orientations in attempt to further elucidate their function. The gorillas in the majority of both control and VP interactions were observed to change their attention (eye, head, or body orientation) toward various points within the environment. It was proposed that VPs are more than moments of rest or inactivity between gorillas and instead, actions occur during these periods that have an impact on how two gorillas further interact with one another and might reflect an important function of play in gorilla socio-cognitive development. VPs may present the opportunity for gorillas to learn about the role of

others' and one's own cues of attention and how these cues can regulate social interactions.

ARs are one especially interesting attentional event in relationship to the overall management of attentional cues. When assessing cues of attention during ARs, gorillas may use these realignments to gather information about the play intentions of a partner or to advertise their own play intentions using postural or behavioral based cues. Such supplemental social information may be contained in the posture of the partner, in the behaviors that the partner is engaged in, and/or in the locomotive movements that a partner may exercise. In this chapter, I will analyze the postural and behavioral contexts of gorilla attentional behavior during VPs in comparison to control rest periods.

1. Postural behavior

Body postures[13] are considered an important component of play research because the posture of an individual can often be an indication of attentiveness or a playful mood (Bekoff, 1995; Flack *et al.*, 2004; Horowitz & Bekoff, 2007; Lazar & Beckhorn, 1974; Pellis, 1997; Petru *et al*., 2009; Rooney *et al*., 2001; Wilson & Kleiman, 1974). In instances where a behavior can span multiple contexts, e.g., mock biting during play versus biting during aggression, the body posture of an animal can clarify contextual ambiguity (Gyóri *et al.*, 2010; Parkinson, 2005). Functional positional behavior studies in the great apes document locomotor and postural behaviors to understand how variations in the positioning of the musculoskeletal anatomy are expressed during

[13] "Postures" in this chapter refer to the stances that the body as a whole occupies, e.g., sit, lie, bipedal stand, etc. This differs from postural references to isolated organs or appendages that are specified in some play research (e.g., ear postures in the American Black Bear: Henry & Herrero, 1974).

particular behaviors (McGrew *et al.*, 1996)[14]. Some cognition studies in the great apes evaluate the role of posture in relationship to handedness (Hopkins, 1993; McGrew *et al.*, 1996), whereas others develop experimental methodologies that evaluate the potential for postural orientations to direct the attention of others to interesting and important events occurring in the environment (Bräuer *et al.*, 2005; Emery, 2000; Emery *et al*., 1997; Kaminski *et al*., 2004; Leavens *et al.*, 2004; Povinelli & Eddy, 1996). Canine and equine cognition studies often gauge attentiveness to an experimental task by the posture that the subject adopts and emphasize the importance of the experimenter's posture in relationship to a subject (*dogs*: Call *et al.*, 2003; Miklósi *et al.*, 1998; *horses*: Proops *et al.*, 2010). For example, the direction of the torso in an orientation toward a dog (Gácsi *et al.*, 2004) or specific postures, sitting (attentive) versus lying (non-attentive), can effectively indicate attentiveness to others (Call *et al.*, 2003; Gaunet & Deputte, 2011). Domesticated dogs are particularly adept at responding to and modifying their behaviors based on postural cues provided by their human owners (Horowitz & Bekoff, 2007).

In many instances, postures dictate the practicality of exercising certain behaviors and some behaviors are better performed from one posture than another, e.g., chest-pounding in gorillas. Two-handed chest-pounding requires the unoccupied hands of a gorilla to strike the chest repeatedly; this cannot be managed if the gorilla is in a quadrupedal posture or if the hands are used to hang from a branch (see postural descriptions in Table 27, I). Similarly, some postures may be easier to transition out of to perform a behavior. A gorilla in a quadrupedal posture can easily chase a partner, whereas a gorilla in a lying

[14] The end goal of these particular studies is typically a better understanding of the advent of bipedalism and locomotive adaptations – and subsequently the communicative adaptations – that occurred in the ape lineage, all of which directly impacted human evolution.

posture has to assume a quadrupedal posture before beginning chase play. Other postures offer extensive possibilities for subsequent behaviors; the play-bow in canids, an exaggerated variation of a quadrupedal stance, allows the dog to move in any number of directions in reaction to an opponent (Bekoff, 1995). Transitioning between postures may also be easier depending on the posture that is occupied. From a lying down posture, a gorilla can transition with ease into sitting upright, whereas the transition from lying down into bipedal standing may be more difficult, and require additional steps and physical effort. Naturally, the postures of gorillas take on individual variations and depend on factors such as context, proximity to group mates, mood, location, etc. (Fig. 36 – Schaller's examples of resting and play postures).

2. Behaviors and movements

The behaviors and movements of gorilla partners during play can also be indicators of a willingness or receptivity to engage in playful interactions (see Table 27, II & III). The exaggeration and non-stereotypical repetition of behaviors and movements has been listed as a criterion of play behaviors (Burghardt, 2005) and can include variations and exaggerations of gaits (e.g., pirouetting, staggered running, and sliding) and repetitive exchanges of behaviors, such as variations on patty-cake and handclapping (personal observations). Previous research has observed that particular behaviors and locomotions occur frequently during the play contexts and may also generate social play between individuals. Squirrel monkeys have been observed to solicit play by looking between the legs (Baldwin & Baldwin, 1974), rats often solicit play by making dorsal contact with a partner (Siviy *et al*., 1997), and canids use a number of approach and withdrawal behaviors to solicit play (Bekoff, 1974). The production of playful behaviors and

movements may not only maintain a playful mood for the actor but also convey playful receptivity to an on-looking partner. The important link between partner attention and the production of a gesture has been highlighted in previous gorilla gestural studies (Genty *et al*., 2009; Tanner, 2004; Tanner & Byrne, 1996, 2010).

3. Study aims

The main aim of Chapter 5 was to expand on the previous chapter's attentional cue analyses and evaluate the postures, behaviors, and movements that accompanied the discrete interaction groupings during control and VP interactions. Chapter 4 indicated the presence of attention cue differences (body, head, and eye gaze) between control and VP interactions, in which VP gorillas produced higher densities of attention changes and trends of partner-directed attention emerged, particularly as play was resumed. The term "vigilance period" suggests a time frame in which partners watch one another's behaviors in anticipation of the possible resumption or termination of play. Based on the attentional "engagement" between partners during VPs suggested by the results of Chapter 4, I predict that mutual engagement during VPs will also be reflected in the relationships between attentional changes and changes in particular postures, behaviors, and movements. Furthermore, mutually engaged VP gorillas should be more responsive than control gorillas that do not exhibit mutual engagement.

These sketches of gorilla postures are unavailable due to copyright restrictions.

Fig. 37 – Above: Observed mountain gorilla (*Gorilla gorilla beringei*) play postures (adapted from Schaller, 1963, pg. 251). **Right:** Observed mountain gorilla resting postures (adapted from Schaller, 1963, pg. 144-45 & 256).

Methods

1. Study site and gorillas

The gorillas and study site were the same 7 western lowland gorillas (*Gorilla gorilla gorilla*) of the Brookfield Zoo in Chicago, IL, USA that were observed in Chapter 4. Information regarding the layout of the gorilla exhibit and further pedigree information about the group members is shown in the preceding methodological section of Chapter 4 in Table 18, pg. 143.

2. Data collection and ethogram compilation

The data collection procedure and sampling methods were the same as those outlined in the methodological section of Chapter 4 (pg. 142). The previously defined control and VP interactions were again analyzed to conduct a comparative analysis of gorilla actions during these two specific interaction types (see Chapter 4, p. 140 for VP diagram). Chapter 4 stated that control interactions were differentiated from VPs as periods of "rest" in which the gorillas had not engaged in social interaction with one another (with the exception of allogrooming) nor had they engaged in play immediately before or after the period of rest. Data for VPs and controls were collected at two fixed intervals, the beginning 1 s and the end 1 s and each time a change in attention occurred. Original ethograms were constructed representing the basic postural and action (behaviors, movements, and monitoring) repertoires of the gorillas from gorilla play video footage and through consultation with a variety of gorilla behavioral ethograms (The Gorilla Behavioral Advisory Group (GBAG), Ogden *et al*., 1991; Pika, 2003) [Table 27].

I.

Postures

Bipedal[1,2,3]	The gorilla is raised up on two legs and either balances (unsupported) or uses a substrate/partner to balance (supported).
Crouch[1,2]	The gorilla is bent at the knees in a squat (unsupported) or uses the hands or forearms to support its body weight (supported).
Hang[1]	Suspension from a branch, rope, or other substrate in the enclosure.
Headstand	The gorilla places the crown of its head on the ground and turns upside down. The head and neck support most of the body weight and balancing is accomplished with the legs and feet.
Lie[1]	A supine, prone, or lateral recumbent position of the body (multiple variations).
Quadrupedal[1]	The gorilla has legs widely spaced and placed underneath the torso perpendicular to the ground. The arms can be either relaxed or rigid and the knuckles (typically) support the weight of the upper body.
Sit[1]	The buttocks touch the ground and the back is perpendicular to the ground.
Upside down	The gorilla positions itself over a substrate (typically a branch) so that its upper body (head, torso, and arms) freely dangles with the head toward the ground and the lower body remains supported by the substrate.

II.

Behaviors

Allogroom[1]	Brushing or picking through a partner's hair with the fingers or lips.
Autogroom[1]	Brushing or picking through own hair with the fingers or lips.
Arm swing[1,3]	The gorilla sweeps an arm out towards a partner then back in toward their body.

Arm wave[3]	The gorilla sweeps an arm in an upward motion toward the shoulder, flexing the elbow joint; a "come here" motion.
Attempt Block[1]	The gorilla puts up the hands or arm to shield direct contact from a partner.
Bite[1,3]	The gorilla places its mouth on the partner and uses the teeth to grip.
Chest-pound[1,2,3]	The gorilla repetitively hits the chest area with one or both hands. The fingers can be outstretched (smacking motion) or cupped into relaxed or tight fists. The gorilla is typically in a bipedal stance while either standing, walking, or running; however, multiple variations are possible.
Coprophagy[1]	The gorilla eats feces.
Drink[1]	The gorilla consumes a liquid.
Drum[3]	The gorilla uses the hands to repetitively tap on their own or a partner's body.
Eat[1]	The gorilla consumes a food source.
Gather[1]	The gorilla sweeps and picks up food, hay, or another item.
Grab[1,2,3]	The hand or foot is placed on a partner's body and the fingers or toes are curled to create a grasping motion.
Grapple[3]	The gorilla places their hands on the head and/or shoulders of the partner and draws the partner's head in close to their own.
Hand clap[1,2,3]	The palms are brought together once or more in rapid succession in the space in front of the gorilla.
Hay display[3]	The gorilla takes hay and in any combination shakes it, throws it, or uses it as a prop to interact with their partner.
Head shake[1,3]	The gorilla moves its head rapidly from side to side (horizontal plane), sometimes involves a protruding tongue.
Head bob[3]	Rapid movement of the hands in front of the face while moving the head from side-to-side and/or up and down. Accompanied by an open mouth face and the tongue may stick out.
Hand shake[2,3]	Rapid movement of the hands, which are typically relaxed and limp at the wrist joints, in front of the torso.

Hit[1,2,3]	The gorilla makes contact with a partner using moderate force. The hands can be open or closed.
Huddle[1,2,3]	Two or more gorillas sit in direct contact (torso to torso, side to torso, back to torso, etc.); the arms and legs may be wrapped around one another (multiple variations).
Inspect[1,2]	The gorilla positions their face and body close to an object of interest. This is performed without making contact and is typically observed with a partner when that partner is eating.
Kick[1,3]	The gorilla uses a foot/feet to strike another.
Lick[1]	The tongue is used to investigate a partner or a substrate surface.
Look[1,3]	The gorilla fixes their eyes on a location, object, or partner in the environment for ≤ 2 seconds.
Manipulate[1]	The gorilla uses the hands or feet to handle and/or investigate an object, partner, or self.
Mouth[1]	The placement of the mouth on a partner or an object without using the teeth (no biting).
Poke[1,3]	An extended finger(s) is jabbed into the body of another.
Pull[2]	The gorilla moves a partner or an object toward them.
Pull away	The gorilla removes his or her own body or an object from the grasp or reach of a partner.
Push/Nudge[1,2,3]	The gorilla uses one or both hands (or feet) and moves their playmate away from them in the opposite direction.
Raise[3]	The gorilla lifts a limb and suspends it in mid-air.
Release[1]	The gorilla lets go of their grasp on an object or a partner.
Reach[1,2,3]	The gorilla extends an arm toward a partner or an object.
Scan	The gorilla moves the eyes around the environment but does not fixate on any one particular entity.
Scratch[1]	The gorilla rubs the fingers/fingernails back and forth and/or up and down along the fur and skin. This can be self-directed or used on a partner.
Shake[1,2,3]	An object or body part is moved rapidly from side-to-side or up and down.

Slap/Beat[1,2,3]	The gorilla hits another forcibly with an open palm.
Somersault[1,2,3]	Turning the body head over heels for one or more full rotation.
Stare[1]	The gorilla focuses their gaze on a partner and the eyes are hard and fixed.
Stomp[2,3]	The gorilla firmly brings the foot/feet down on the ground.
Stop	The gorilla ceases the activity they are engaged in.
Take[1]	One gorilla seizes food or an object from another.
Tap[1,3]	The gorilla uses the knuckles to strike a substrate or an object.
Throw[1,2,3]	The tossing of an external object anywhere (i.e., hay, plastic ball, etc.).
Tongue Wag	An open mouth with the tongue sticking out and moved rapidly from side to side.
Touch[1,2,3]	Use of the hand or foot to gently contact a partner or object.
Wall/Ground/Object slap[1,2,3]	The gorilla strikes a substrate or object with one or both hands. The strike may be with open palms, back of the hands, or sides of the fists.
Watch[1]	The gorilla fixates on and observes a partner for ≥ 2 seconds.
Water[1,3]	Wading into or splashing of self or others in an enclosure water source.

III.

Movements

Adjust	The gorilla fidgets with or superficially moves an object, himself/herself, or an element of the surrounding environment after an already established orientation or placement.
Chase[1]	One gorilla rapidly follows another with an exaggerated running gait.

Climb[1]	Scaling up or down of any substrate in the enclosure.
Dangle	The gorilla is suspended in either a hang or upside down posture above the ground (typically with the belly over a branch) and freely moves the arms or legs.
Fall over[1]	The gorilla topples from a posture or a movement onto a supporting structure or the ground.
Flinch	The gorilla makes a quick reflexive movement away from the direct contact of a partner.
Head down	Lowering of the head and shoulders exposing the crown of the head to the partner, typically seen at the resumption of play before engaging in a behavior e.g., grappling.
Lean over[1]	The gorilla rigidly tilts their upper body and lessens the angle between their upper body and the ground. This is typically performed while in a seated position and can be in any direction.
Lie on	A supine, prone, or lateral recumbent position on a partner or raised object e.g., branch, log, etc.
Lie down[1]	Transition from a standing or sitting posture into lying posture.
Move away	An increase in distance > 1 m between the partners by locomotion of a gorilla in a direction opposite from the partner.
Move back	An increase in distance between the partners by 1m or less by locomotion of a gorilla in a direction opposite from the partner.
Move forward	At a starting distance of 1m or less, the gorilla locomotes toward the partner and decreases the distance between them.
Move to[1]	At a starting distance of more than 1m, the gorilla locomotes toward the partner and decreases the distance between them.
Roll[1,3]	The gorilla turns the body from one side to the other while lying, and the rotation can be complete (360º) or incomplete. This can be in the direction of the partner (roll to) or away from the partner (roll away).
Roll over	From a standing, sitting, or lying position the gorilla rolls into a relaxed fetal position.
Sit back	The gorilla slightly scoots their sit posture away from their partner but remains ≤ 1m away from their partner.
Sit down	From a bipedal or quadrupedal position, the gorilla sits on their buttocks.
Sit up	From a head down orientation or a lying position, the gorilla raises their torso and head and adopts the sit posture.

Stand to Quad[1]	The gorilla transitions from a lying or seated position into a quadrupedal stance.
Stand to Bipedal[1]	The gorilla transitions from a seated, lying, or quadrupedal stance into a bipedal stance.
Swing[1]	Motion of the gorilla above the ground from one location to another via pseudo-brachiation or a rope.
Turn away[1]	The rotation of the body in a direction opposite of the partner.
Turn to	The rotation of the body in a direction toward the partner.
Twirl/Pirouette[1,2,3]	Spinning around in one or more circles either quadrupedally or bipedally.
Walk[1]	Quadrupedal or bipedal slow paced locomotion.

Table 27 – The three ethograms: postures (I), behaviors (II), and movements (III) with the name (in bold) and corresponding description. The study author (JM) developed the descriptions of the behaviors. (1) Denotes a similar posture/behavior/movement description (may have a different name) from a GBAG ethogram, (2) denotes a similar posture/behavior/movement description (may have a different name) in the Pika *et al.* (2003) ethogram, and (3) denotes a similar posture/behavior/movement description (may have a different name) in the Genty *et al*. (2009) ethogram.

Overall, eight general **postures** were observed in gorilla social interactions: *bipedal*, *crouch*, *hang*, *headstand*, *lie*, *quadrupedal*, *sit*, and *upside down* (Table 27, I). The postures for each gorilla were recorded at specific intervals during the interactions, namely the beginning and end of each interaction and then simultaneously (≤ 1 second time frame) each time a gorilla performed an attentional change (e.g., the gorilla oriented their head toward their partner while in a sit posture).

In addition to postural data, gorilla actions were compiled and general categories were derived from the data:

1) the **behaviors** of each gorilla partner were recorded at the beginning, end, and at any attention change that occurred during the interaction (Table 27, II). Occasionally, more than one behavior (e.g., grab hay and throw hay) was observed to accompany an attention change, and each behavior was recorded accordingly. These actions could be self-directed or directed toward a partner;

2) observations of locomotion and body movements resulting in postural changes were combined under the **movements** category (Table 27, III) because these actions all pertained to gorilla bodies in motion. Body movements that resulted in postural changes were included when the gorilla's body action resulted in a change from one of the above-mentioned postures to another (e.g., stand to quad, lie down, etc.) and were recorded as an active change in posturing and not the static posture itself;

3) **monitoring** behaviors included: *look*, *scan*, *stare*, and *watch*. These behaviors were

observational in nature and pertained to the monitoring of a partner, surrounding group mates, or the environment. These behaviors were only recorded as such when eye gaze of the gorilla could be observed; and

4) the gorilla was categorized as at **rest** if it was not observed to perform an action that could be categorized as one of the above three actions.

3. Data analysis

Statistical analyses were performed in IBM SPSS 19.0. The initial analyses of Chapter 4 showed that the frequencies in the changes of attention direction were variable throughout control and VP interactions. Therefore, the analyses of the postural and action data (inactivity, behaviors, movements, and monitoring) were organized similarly to the data analyses outlined in the methodology of Chapter 4, and the gorilla interactions (both controls and VPs) were initially arranged into two broad attentional groups:

1) where the gorilla engaged in either 0 or 1 AT, e.g., they oriented their attention away from their partner at the start of the interaction and remained averted for the duration of the interaction; or

2) where the gorilla engaged in an AR, e.g., the gorilla oriented their attention away from their partner and then reoriented back toward their partner.

Control and VP postural data were analyzed initially (results section 1) based on the categorization of the interaction into one of the two above outlined attentional groups (containing an AT or AR) [Fig. 37].

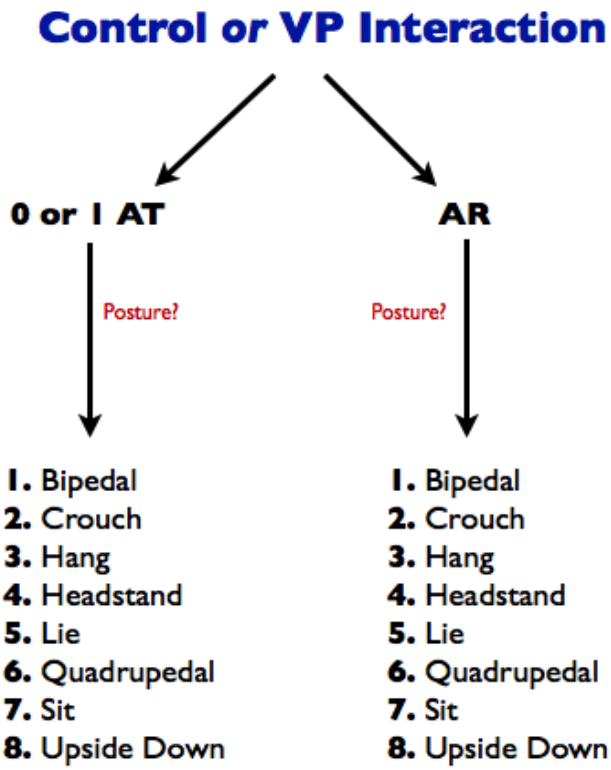


Fig. 38 – The categorization of control and VP postural data by attention change category (AT or AR) for the further analyses of each interaction type.

The gorilla actions were then analyzed (results section 2) through further categorization and a multi-step procedure (Fig. 38) creating smaller subsets of control and VP data. Actions were also initially categorized based on the frequencies of attention changes (ATs or ARs). ATs and ARs were then additionally sub-divided into two separate groups based on: 1) the actions of the gorilla that **performed** a change in attention and 2) the actions of the partner gorilla that the attention change was **directed toward**. These two subsets of data were analyzed separately. The actions of the partner gorilla that an attention change was directed toward were deemed an equally important analysis to develop a complete understanding of the context that surrounded attention changes (or in some cases, 0 ATs). The actions of each gorilla partner – either the gorilla that engaged in the attention change or the recipient gorilla of the attention change – were then further

organized into: the 1) **recipient** of a partner action or 2) the action **performer**. The actions of both the recipient and the performer were then finally broken down into: 1) **inactivity/rest**, 2) **behaviors**, 3) **movements**, or 4) **monitoring**. When a 2nd behavior was observed it was also recorded (e.g., gather hay and eat) and categorized accordingly. Both 1st and 2nd actions were then tallied and analyzed to identify the frequencies of inactivity/resting, specific behaviors, specific movements, and monitoring that occurred within controls and VPs.

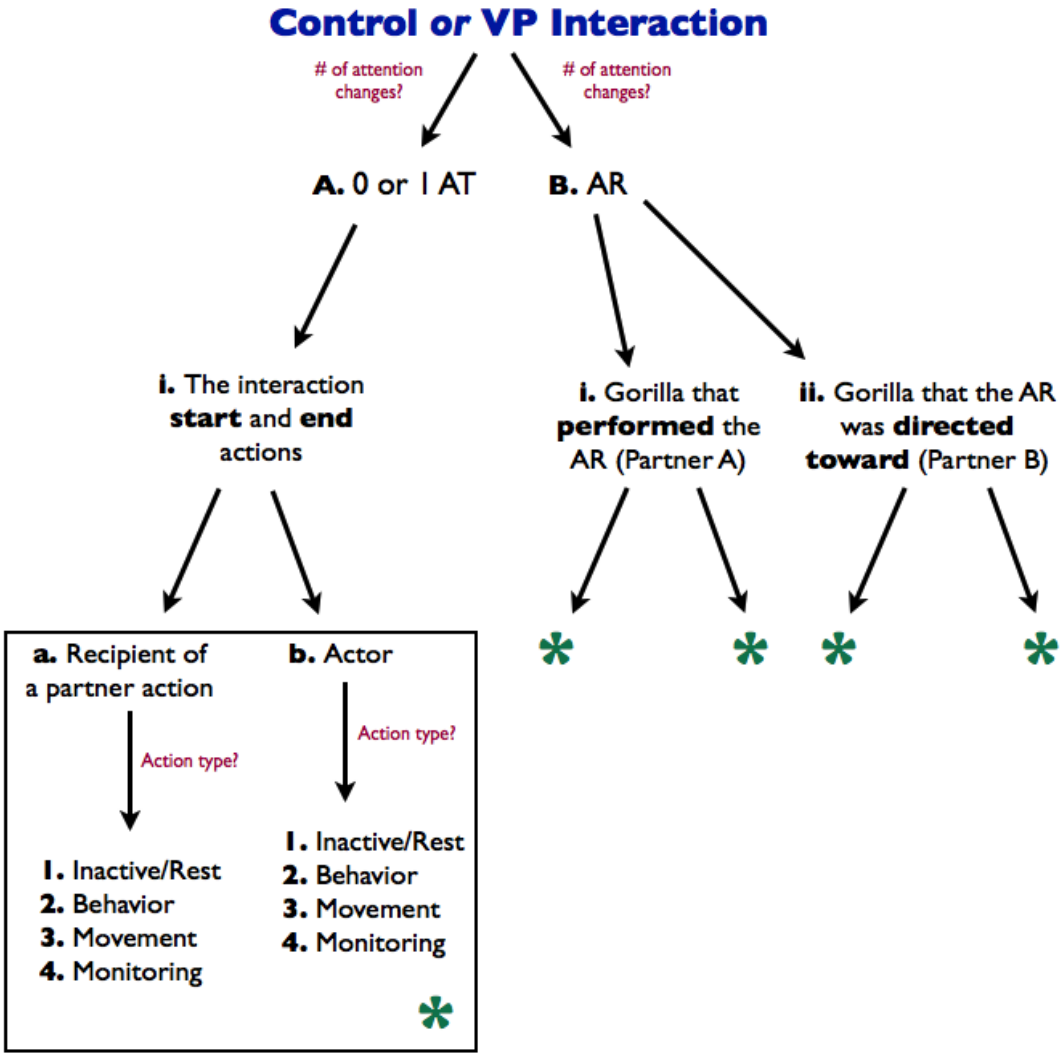


Fig. 39 – The step-wise categorization of action data for the analysis of control and VP interactions. The asterisked groups for the AR subsets also followed the same sub-categorization represented in the asterisked box.

Results

Section 1 of the results analyzes the gorilla postures during interactions with 0-1 AT (1.1) and interactions containing ARs (1.2). These analyses focus on the starting and ending postures (1.1 and 1.2) and the postures that occur simultaneously (≤ 1 second time frame) with an attentional change (1.2) to determine if gorilla posturing differed during control and VP interactions with variable amounts of attention changes. Section 1.3 provides a summary of the postural results in section 1 (Fig. 40).

1. Gorilla Postures
- **1.1.** Postures during interactions with 0-1 AT
- **1.2.** Postures during interactions with ARs
- **1.3.** Summary

2. Action(s) of the gorillas during controls and VPs
- **2.1.** Gorillas engaged in interactions with 0-1 AT
  - **2.1.1.** Recipient of a partner action
  - **2.1.2.** Actor (the gorilla that performed an action)
    - **2.1.2.1.** *Inactive/Resting*
    - **2.1.2.2.** *Behaviors*
    - **2.1.2.3.** *Movement*
    - **2.1.2.4.** *Monitoring*
  - **2.1.3.** Summary
- **2.2.** Gorilla dyads engaged in ARs: the actions of the AR performing gorilla
  - **2.2.1.** Recipient of a partner action
  - **2.2.2.** Actor (the gorilla that performed an action)
    - **2.2.2.1.** *Inactive/Resting*
    - **2.2.2.2.** *Behaviors*
    - **2.2.2.3.** *Movement*
    - **2.2.2.4.** *Monitoring*
  - **2.2.3.** Summary
- **2.3.** Gorilla dyads engaged in ARs: the actions of the gorilla the AR was directed toward
  - **2.3.1.** Recipient of a partner action
  - **2.3.2.** Actor (the gorilla that performed an action)
    - **2.3.2.1.** *Inactive/Resting*
    - **2.3.2.2.** *Behaviors*
    - **2.3.2.3.** *Movement*
    - **2.3.2.4.** *Monitoring*
  - **2.3.3.** Summary

Fig. 40 – The structure of the analyses conducted in the results section.

Section 2 is broadly divided into three sub-sections (2.1, 2.2, and 2.3) that analyze the actions of the gorillas during controls and VPs with variable amounts of attention changes. Sub-section 2.1 analyzes the actions of gorilla dyads during controls and VPs with 0-1 AT and focuses on the start and end actions of both the action recipient (section 2.1.1) and the action actor (2.1.2). The actions of the gorilla actor could be further categorized into inactivity/rest (2.1.2.1), behaviors (2.1.2.2), movements (2.1.2.3), or monitoring (2.1.2.4) to determine the overall behavioral states of each gorilla during interactions with 0-1 AT.

Sub-section 2.2 analyzes the actions of the control or VP gorilla that performed an AR. The analyses focus on actions that occurred at the beginning, end, and at the simultaneous moment an AR occurred. The gorilla that performs an AR could either be the recipient of an action from a partner (2.2.1) or perform an AR while simultaneously performing an action (2.2.2) that could be categorized as inactivity/rest (2.2.2.1), behaviors (2.2.2.2), movements (2.2.2.3), or monitoring (2.2.2.4). These analyses were conducted to determine whether the performance of an AR corresponded with particular gorilla activities and whether there was a difference in activities between control and VP gorillas.

Sub-section 2.3 analyzes the actions of the control or VP gorilla that was the recipient of an AR. The analyses again focus on actions that occurred at the beginning, end, and at the simultaneous moment an AR occurred. The gorilla that an AR was directed toward could either also be the recipient of an action from the AR performing partner (2.3.1) or

could be simultaneously performing an action that an AR was directed toward (2.2.2). Again, these actions could be categorized as inactivity/rest (2.3.2.1), behaviors (2.3.2.2), movements (2.3.2.3), or monitoring (2.3.2.4). These analyses were conducted to determine whether ARs were directed toward a partner that was engaged in a particular activity and whether there was a difference in the activity levels between controls and VPs.

1. Gorilla Postures

1.1. Postures during interactions with 0-1 AT

Control and VP interactions that contained 0-1 AT (*controls*: $n = 8$; *VPs*: $n = 48$) had measurable postural data for two comparable time frames, i.e., the beginning and end points of each interaction. At the beginning time frame of both controls and VPs, *sit* occurred more often than any other posture (*controls*: 62.5%, $n = 10$; *VPs*: 60.4%, $n = 58$) and *bipedal* and *hang* were only observed at VP beginnings. At the end of control interactions, gorillas were observed in *lie* (43.8%, $n = 7$) and *sit* postures (37.5%, $n = 6$), and VP gorillas were most often observed in a *sit* posture (56.2%, $n = 54$) at the end of VPs [Fig. 41].

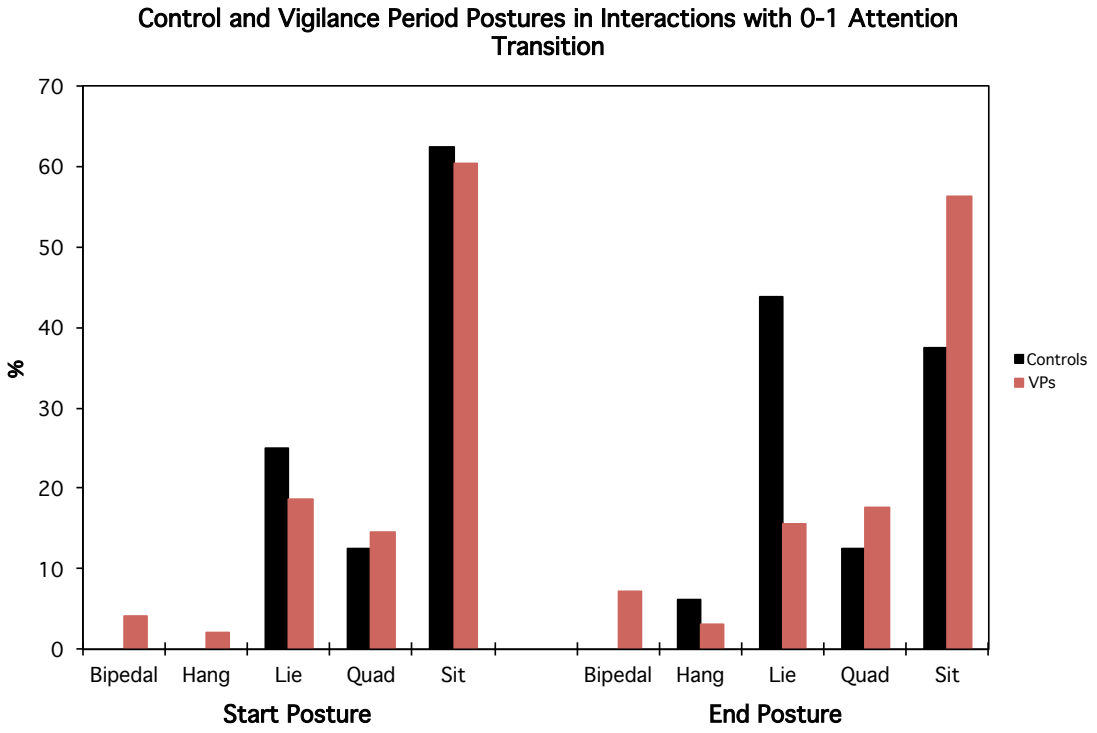


Fig. 41 – The start and end postural positions for gorillas at the beginning and end time frames of controls and vigilance periods with 0-1 attention transitions (AT). Sitting was the dominant postural position for both interaction types at the start of the interaction.

Controls and VPs were then further investigated to determine whether the same posture was maintained at the beginning and end time frames or whether a postural change occurred. Postural switching and maintaining the same beginning and end posture occurred in comparable amounts in both interaction types (*Wilcoxon signed-ranks test*: $z = -.9$, $p > .05$). When control gorillas performed postural switching it was in low amounts ($n = 5$). VP gorillas most often transitioned from a *lying* (30.8%) or a *sit* (38.5%) posture into a *quadrupedal* (30.8%) or *sit* (44.2%).

1.2. Postures during interactions with ARs

In interactions where ARs were present (*controls*: $n = 55$; *VPs*: $n = 253$), postural differences were again evaluated at the start and end time frames and then at each AR

throughout the duration of the interaction. Overall, both control and VP gorillas were most frequently in a *sit* posture (*controls*: 67.5%, *n* = 767; *VPs*: 62.8%, *n* = 1924) or *quadrupedal* posture (23.4%, *n* = 717). *Crouch* and *headstand* postures were only observed during VPs, and *bipedal* and *hang* postures occurred more frequently throughout VPs (4.5% and 1.3%, respectively) than controls (Fig. 42).

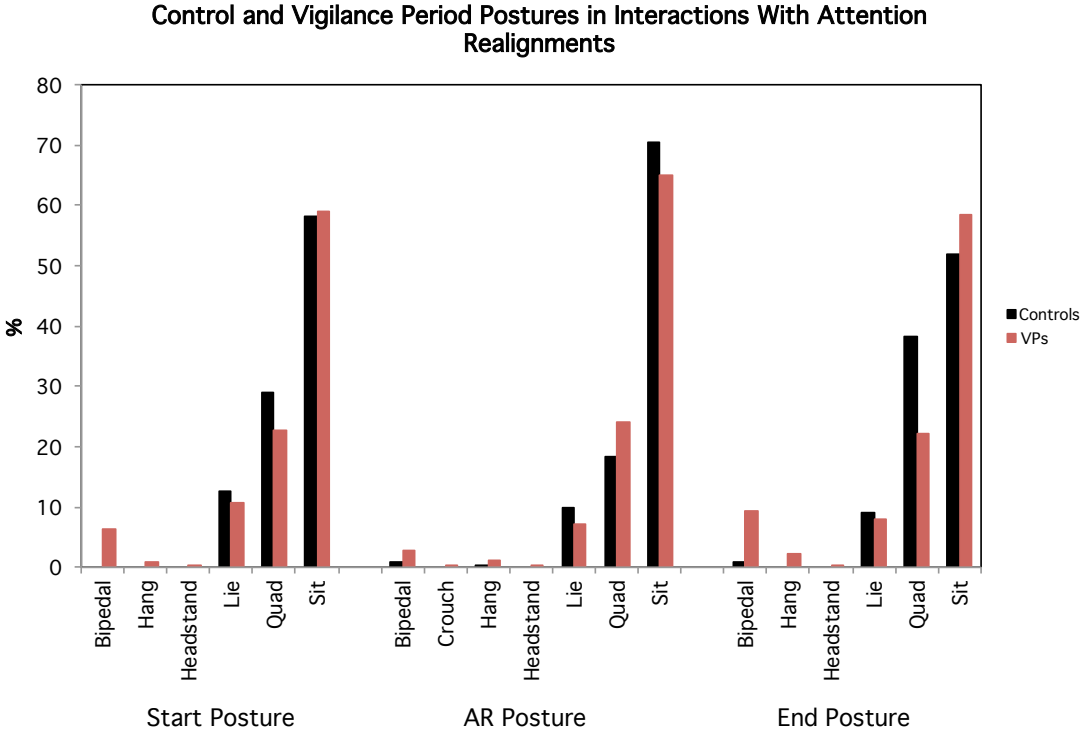


Fig. 42 – A breakdown of posture frequencies at the start, during attention realignments (ARs), and at the end of controls and vigilance periods. *Sitting* was the most frequently observed posture for all three time frames of both interaction types.

Changes between postures were also analyzed as they occurred throughout interactions containing ARs. Postural switching occurred in low amounts during both controls (11.3%, *n* = 116) and VPs (15.0%, *n* = 384). The highest number of postural changes in controls was 6 (observed in 1 interaction), and the highest number of postural changes was 8 in VPs (0.4%, Fig. 43).

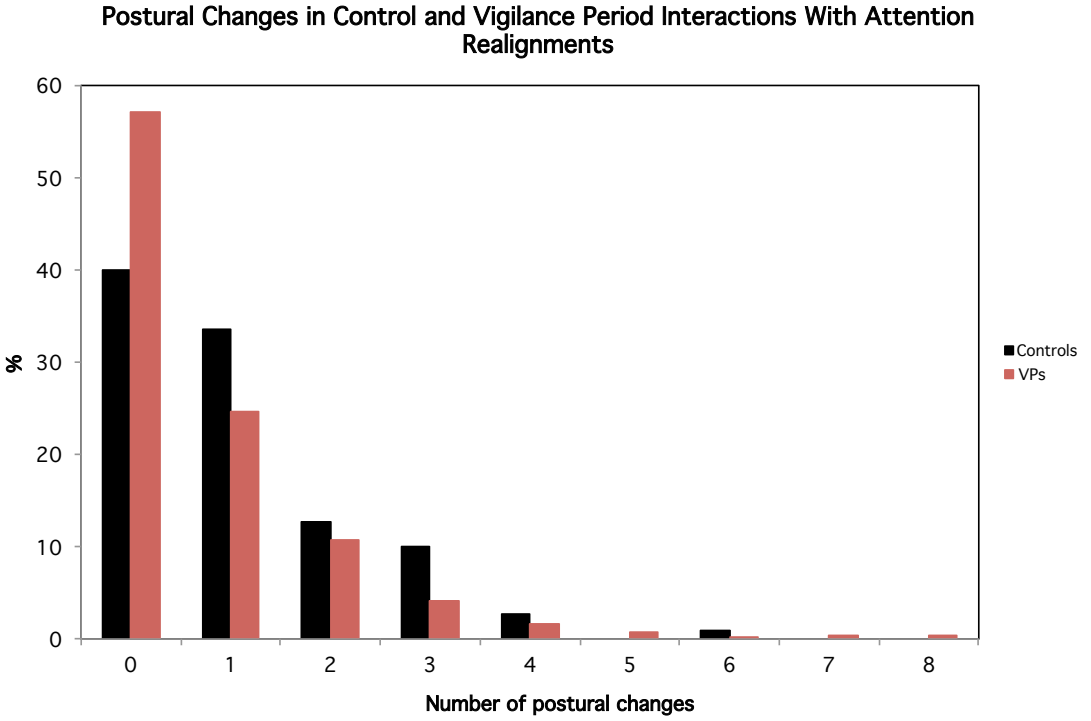


Fig. 43 – The number of postural transitions that occurred in control and vigilance period interactions containing attention realignments.

In controls, 60.5% of postural changes occurred between *sit* and *quadrupedal* postures and 91.2% of changes were either from or into a *sit* posture. VP gorillas were also frequently *sitting* with 77.5% of transitions either from or into a sitting posture. VPs contained a higher transitional rate from or into a *bipedal* posture (29.4%) than controls (11.4%).

1.3. Summary

Overall, *crouch* and *headstand* postures were exclusive to VPs, and *hang* and *bipedal* postures were used more often during VPs than controls. The postural frequencies at the beginning of 0-1 AT interactions in both controls and VPs were comparable for all postural types. However, at the end of 0-1 AT interactions, *bipedal* and *hang* postures

were only observed in VPs, control gorillas more frequently used a *lie* posture, and VP gorillas were most frequently *sitting*.

In interactions with ARs, a significant difference was observed between controls and VPs for the overall frequency of observed postures; control gorillas were most frequently *sitting* and VP gorillas were most frequently *sitting* or *quadrupedal*. These results indicate that some postures, *crouch*, *headstand*, *bipedal*, and *hang*, might be used more frequently within the play context than during controls and that gorillas might be inclined to utilize a variety of postures during VPs.

2. Action(s) of the gorillas during controls and VPs

2.1. Gorillas engaged in interactions with 0-1 AT

Control and VP interactions that contained 0-1 AT (*controls*: n = 8 cases; *VPs*: n = 48 cases) were isolated for separate analysis from those that contained ARs. Again, this subset of cases had data that were measurable for two time frames, the beginning and end points of the interaction, and the actions from both time frames were recorded and totaled for the overall frequencies of actions observed in interactions with 0-1 AT (Table 28).

	Controls		Vigilance Periods	
	0 Attention Transitions	**1 Attention Transition**	**0 Attention Transitions**	**1 Attention Transition**
2.1.1. Recipient of a partner action	-	-	9.5% (9)	7.2% (9)
2.1.2. Actor				
1. Inactive/Resting	11.1% (1)	41.6% (10)	17.9% (17)	13.7% (17)
2. Behaviors	77.8% (7)	29.2% (7)	29.5% (28)	29.0% (36)
3. Movement	11.1% (1)	29.2% (7)	43.1% (41)	49.2% (61)
4. Monitoring	-	-	-	0.8% (1)
Totals	**9**	**24**	**95**	**124**

Table 28 – The proportions (%) with counts (*n*) in parentheses of the actions that gorillas performed for each sub-category of control and vigilance period interactions (0 or 1 attention transition). Control interactions contained fewer cases than VPs (overall *n* values), which made direct comparison difficult in some instances.

2.1.1. Recipient of a partner action

There were no recorded instances within the 0-1 AT control subset where a gorilla performed an action on their partner. However, VPs contained 18 observations (28 actions, Table 28) in which one gorilla acted on the other during the VP. In all cases, this action occurred at the end of the interaction and was most often a *bite* (25.0% of recipient actions, $n = 7$) or *grab* from a partner (21.4%, $n = 6$).

2.1.2. Actor (the gorilla that performed an action)

2.1.2.1. *Inactive/Resting*

Control and VP gorillas were observed to be either active, i.e., behavior, movement, or monitoring, or inactive, "resting", in which they exhibited no overt actions during the interaction and data were only assessed for the start and end time frames. Resting gorillas occurred in comparable amounts in both controls and VPs with 0-1 AT (*Paired samples t-test*: $t_{(5)} = -1.4$, $p > .05$). Active gorillas occurred in comparable amounts in

both controls and VPs with 0-1 AT (*Paired samples t-test*: $t_{(4)} = -1.9$, $p > .05$). In all interactions (0-1 AT), control gorillas were most frequently observed to rest in a *lie* posture (72.7% of the total observed resting postures), whereas VP gorillas were more frequently in a *sit* posture (66.7%).

2.1.2.2. *Behaviors*

In cases where 0 ATs occurred, 3 behaviors were observed during controls, and 14 were observed during VPs. The behaviors *gather hay* and *handclap* were observed in both controls and VPs. Control gorillas were most frequently observed eating ($n = 5$), whereas VP gorillas engaged in *bite partner*, *grab partner*, or *grapple partner* the most (17.8%, $n = 5$) [Fig. 43].

In control interactions where 1 AT occurred, 3 behaviors were observed (*autogroom*, *inspect branch*, and *eat*) [Fig. 44]. Again, VP gorillas engaged in a variety of behaviors, including *grab partner* (36.1%, $n = 13$), *bite partner* (19.4%, $n = 7$), etc. For combined interactions with 0-1 AT, VP gorillas were engaged in 18 total behaviors whereas control gorillas exhibited only 5 behaviors.

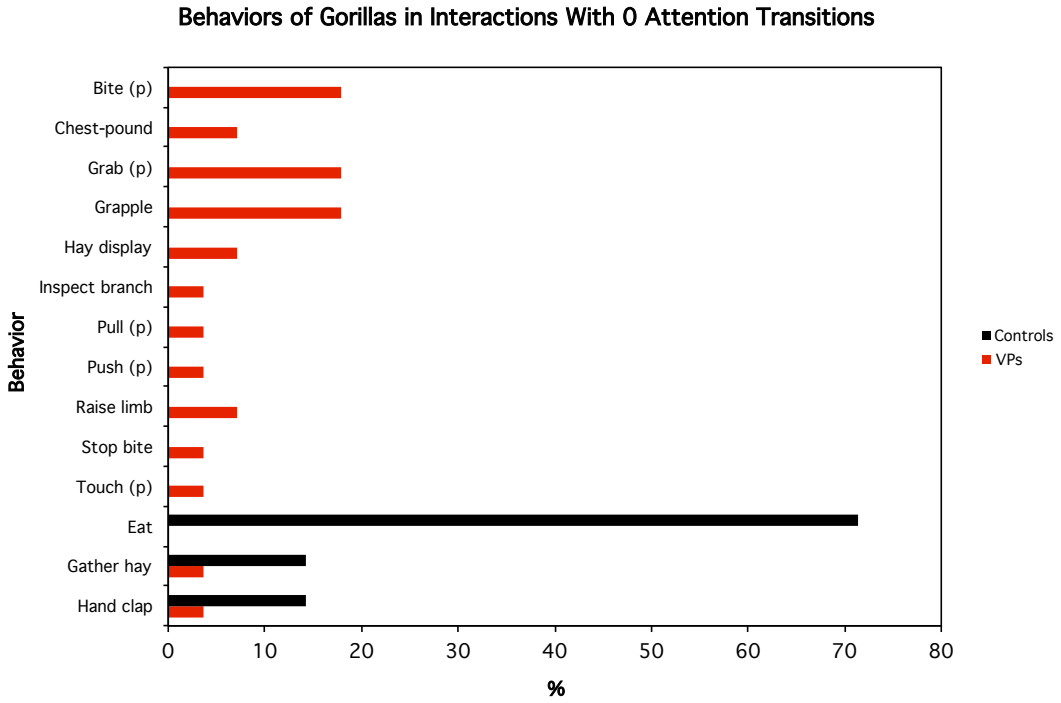


Fig. 44 – The proportions of observed behaviors performed by control and vigilance period gorillas that were engaged in interactions with 0 attention transitions. Three behaviors were observed in controls and 14 in VPs.

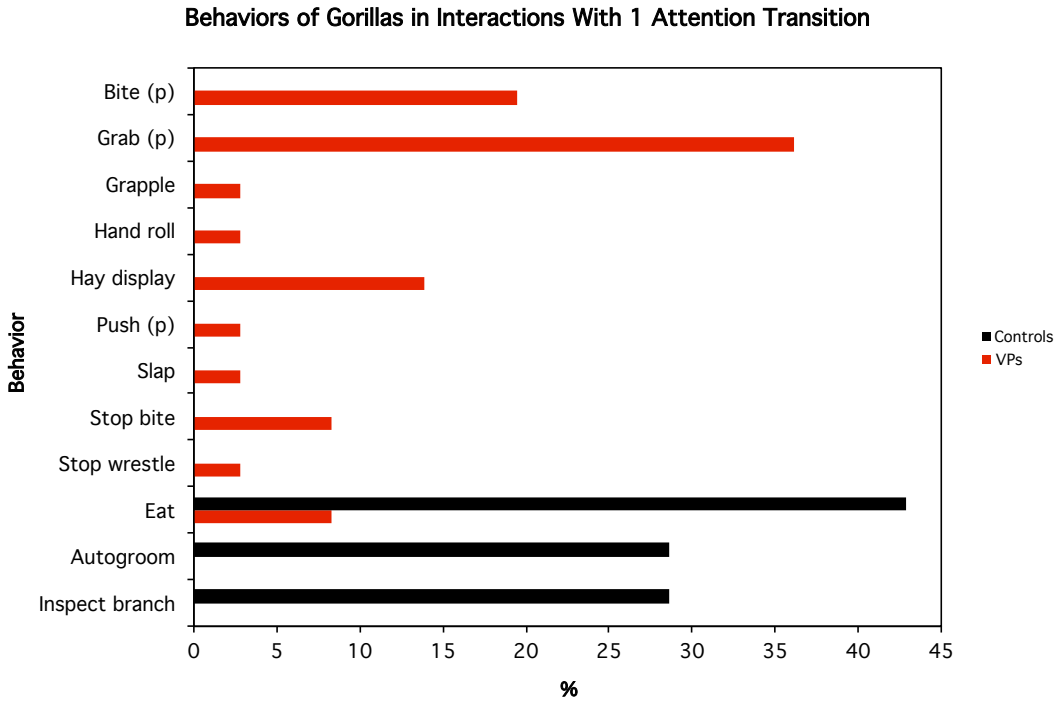


Fig. 45 – The proportions of observed behaviors for control and vigilance period gorillas engaged in interactions with 1 attention transition. Three behaviors were observed in controls and 11 in VPs.

Overall, gorillas exhibited more behaviors during VPs than during controls. Few behaviors overlapped between interaction types, and overlapping control behaviors often occurred in low frequency during VPs (e.g., *autogroom*, *eat*, and *inspect branch*). Behaviors that involved direct contact between the gorilla partners were not observed in control interactions (with 0 or 1 AT). Conversely, 71.9% of behaviors during 0-1 AT VPs involved direct contact with a partner. When a gorilla performed a direct contact behavior, they were already oriented toward their partner in 52.3% of the behaviors, or they oriented their attention (an AT) toward their partner in 34.1% of the behaviors. Audible or visible behaviors were infrequently observed during controls (1 *handclap* occurred in a control interaction with 0 ATs) and occurred more frequently in 0-1 AT VPs (38.9% of observed behaviors). When a gorilla performed an audible/visible behavior, they were already oriented toward their partner in 76.9% of the behaviors; in the remaining behaviors, the gorillas oriented themselves toward their partner and performed the behavior (23.1%). In 61.5% of audible/visible behaviors, the partner was oriented toward the audible/visible behavior.

In all 0-1 AT interactions, controls frequently performed a behavior from a *sit* posture (92.8%, $n = 13$). VP gorillas performed behaviors most frequently while *sitting* (66.1%); however, behaviors occurred from 5 additional postures (*bipedal* = 13.8%; *hang* = 3.1%; *lie* = 12.3%; *quadrupedal* = 4.6%).

2.1.2.3. *Movement*

Gorilla movement was established as locomotion from one location to another and body

movements resulting in postural changes. Only 1 movement was observed in control interactions with 0 ATs (*move away*, $n = 1$). More movements were performed during VPs, and the most frequent movement was *lie on* (28.6%, $n = 10$) [Fig. 46].

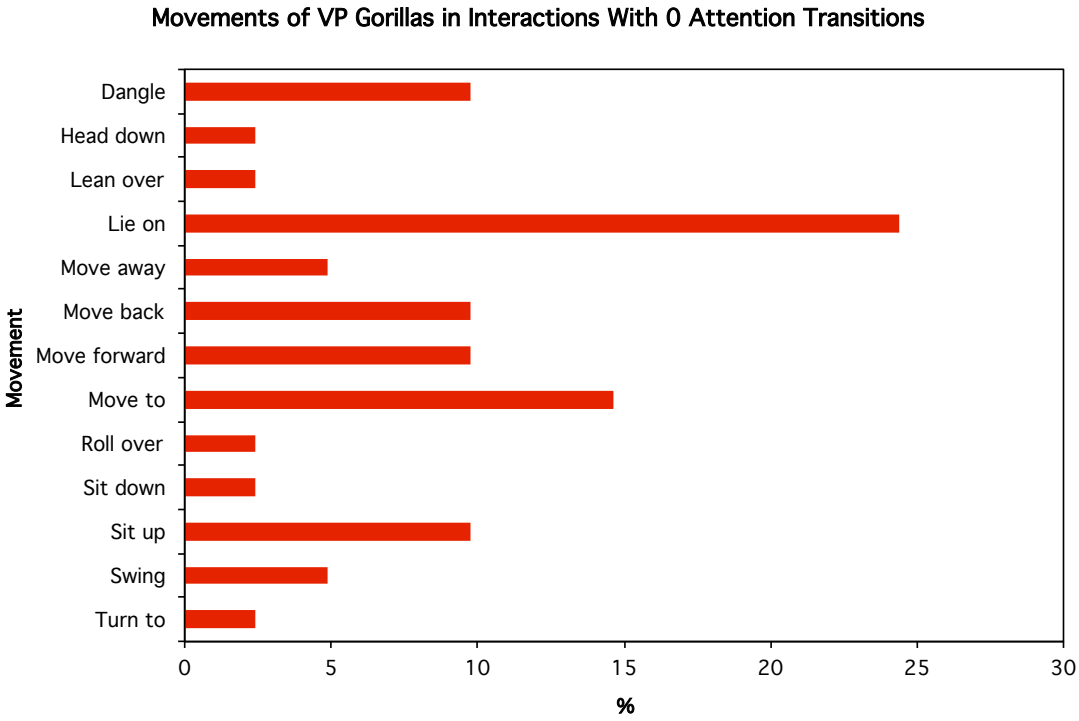


Fig. 46 – The proportions of observed vigilance period gorilla movements during interactions with 0 attention transitions. Control movements were not included in the graph because only 1 movement was observed once (*move away*, $n = 1$).

In interactions where 1 AT occurred, 3 movements were observed in controls (*lie on*, *move away*, and *move to*) whereas 13 movements were observed in VPs [Fig. 46]. Control gorillas were observed to *move away* most frequently (42.8%, $n = 3$) and VP gorillas most frequently performed *sit up* (28.8%, $n = 17$). Overall, VP gorillas exhibited a greater variety of movements than controls. Control gorillas performed the most movements from a *lying* or *quadrupedal* (37.5%) posture, which corresponded with the *lie on*, *move away*, and *move to* movements that were observed. VP gorillas were most often in a *sit* posture while performing a movement (46.3%).

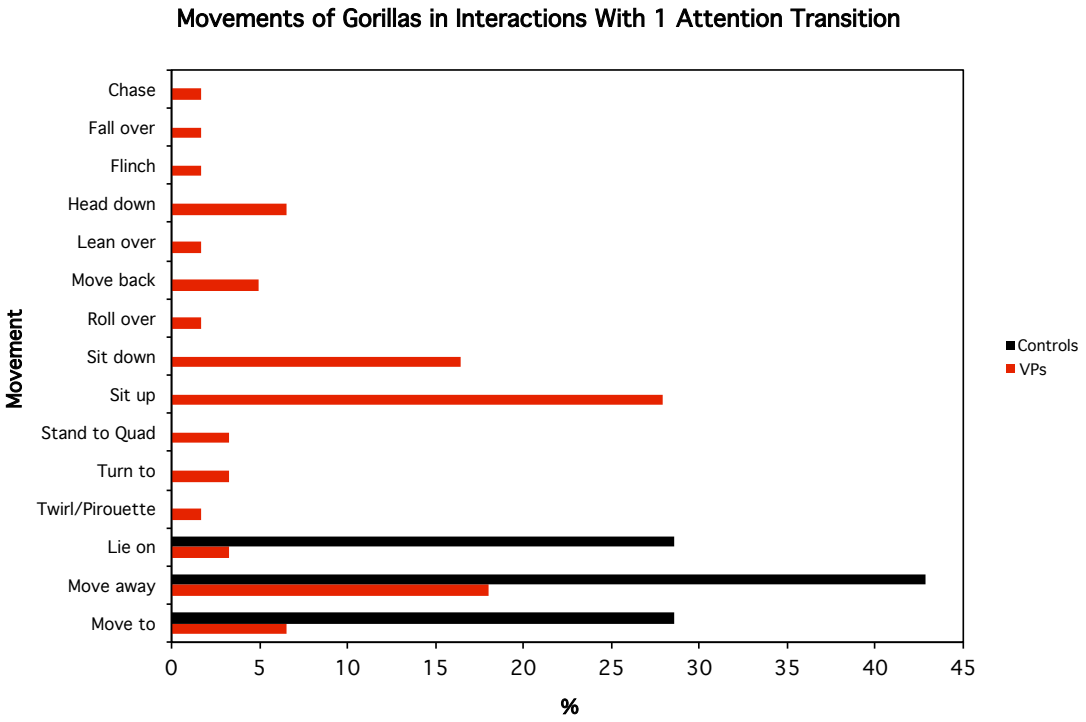


Fig. 47 – The proportions of observed movements of control and vigilance period gorillas engaged in interactions with 1 attention transition.

2.1.2.4. *Monitoring*

Monitoring was not observed in either control or VP interactions with 0 ATs and was only observed once in a VP interaction that contained 1 AT (the gorilla watched their partner *fall over*).

2.1.3. Summary

In interactions with 0 ATs, the amount of resting gorillas displayed was comparable between controls and VPs, but the variability and amounts of observed behaviors and movements were greater in VPs than controls (i.e., higher diversity of types of behaviors and movements). These behavior and movement trends were similar for interactions with 1 AT, and the amount of resting gorillas displayed was also significantly higher in VPs

than controls. Overall, VP resting, behaviors, and movements were also performed from a greater variety of postures (*bipedal*, *hang*, *quad*, *lie*, and *sit*) than controls.

2.2. Gorilla dyads engaged in ARs: the actions of the AR performing gorilla

The analyses of this section investigated the actions that were performed by the gorilla that also performed an AR during controls and VPs. Subsets of 55 control and 301 VP interactions were analyzed, which resulted in a comparison of 458 ARs performed by control gorillas and 1,026 ARs performed by VP gorillas. A total of 472 control actions and 1,062 VP actions were observed (Table 29).

	Controls		**Vigilance Periods**	
	n	**%**	***n***	**%**
2.2.1. Recipient of a partner action	-	-	2	0.2
2.2.2. Actor				
1. Inactive/Resting	165	34.9	580	54.6
2. Behaviors	210	44.5	216	20.3
3. Movement	95	20.1	244	23.0
4. Monitoring	2	0.4	20	1.9
Totals	**472**		**1,062**	

Table 29 – The counts (*n*) and corresponding proportions (%) of the actions that a gorilla performed while also performing an attention realignment for each sub-category of control and vigilance period interactions.

2.2.1. Recipient of a partner action

When a gorilla performed an AR during controls, no instances were observed where the AR occurred simultaneously with an action from the control partner (i.e., the gorilla that performed the AR also performed all of the actions that occurred during controls). In the VP cases analyzed, 2 ARs were observed to have occurred with a simultaneous action

from the VP partner. In both cases, the attention of the gorilla was redirected back toward the partner when they were physically contacted (1st case: partner *grabbed* and *pulled*; 2nd case: partner *pushed*).

2.2.2. Actor (the gorilla that performed an action)

2.2.2.1. *Inactive/Resting*

The gorilla that performed an AR was observed to be actively performing an action, e.g., behavior, movement, or monitoring, or at "rest", in which they exhibited no overt actions except for the AR toward their partner.

Attention realigning gorilla	Partner gorilla	Control frequency	VP frequency
Resting	Resting	14.2% (65)	36.6% (374)
Resting	Active	15.3% (70)	21.9% (224)
Active	Resting	24.4% (112)	21.2% (217)
Active	Active	46.1% (211)	20.3% (207)

Table 30 – The resting/active proportions of the gorilla dyad during control and vigilance period attention realignments.

VP gorillas were at rest while performing an AR (58.5%, n = 598) more often than control gorillas (29.5%, n = 135). ARs occurred between two resting gorillas more frequently during VPs (36.6%, n = 374) than controls (14.2%; n = 65) [Table 30]. Direct contact between the resting AR performing gorilla and their partner were observed in similar frequencies for both controls and VPs (*controls* = 28.5%; *VPs* = 30.5%). Both control and VP gorillas were also most often in a *sit* posture when performing an AR at rest (*controls* = 75.1%; *VPs* = 79.3%).

2.2.2.2. *Behaviors*

Twenty-two behaviors were observed in control ARs, and 24 behaviors were observed in VP ARs; 9 of these behaviors were observed in both interaction types (*eat*, *gather hay*, *grab*, *hand clap*, *hold*, *inspect*, *pull*, *push*, and *touch*). In both controls and VPs, the gorilla that performed an AR was also most frequently engaged in eating (*controls* = 27.7%, *VPs* = 9.8%) [Fig. 47]. Control gorillas performed an AR with a behavior most frequently while in a *sit* posture (82.8% of postures observed). VP gorillas were also observed to utilize *sit* (70.4%) frequently when performing an AR and a behavior. *Crouch* was only observed in VPs (0.5%), and *quadrupedal* and *bipedal* occurred more frequently in VPs than controls (16.7% and 6.0%, respectively).

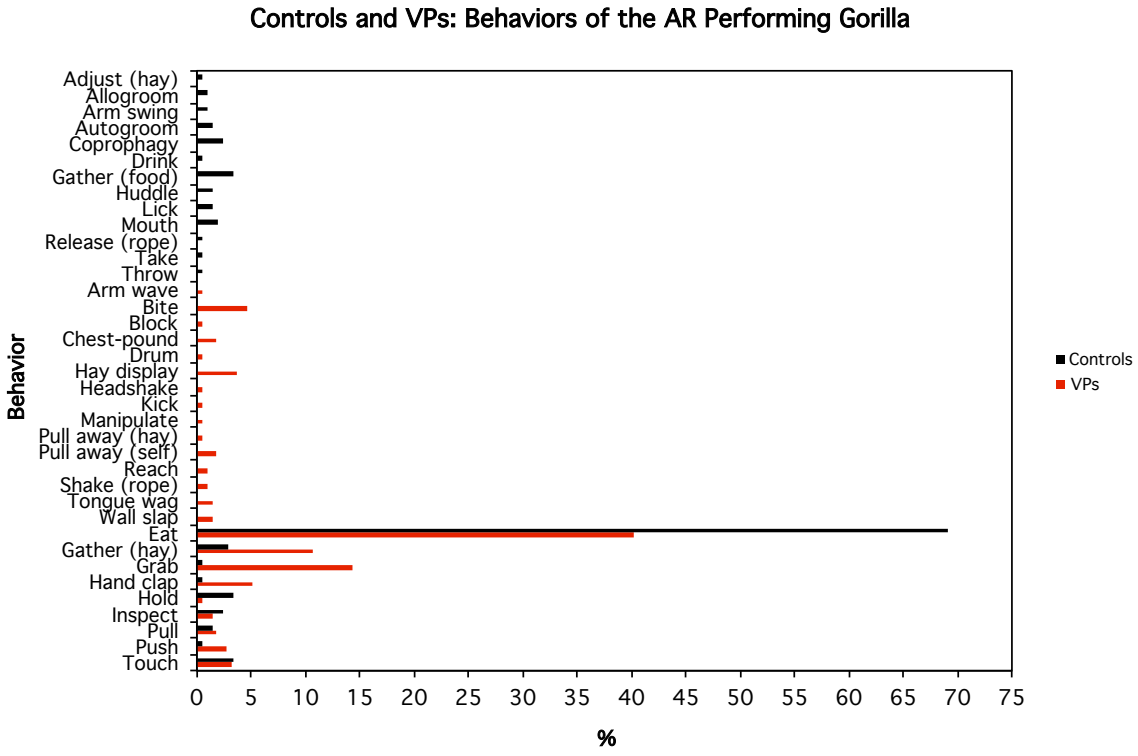


Fig. 48 – The behaviors of the gorilla that performed the attention realignment. Nine behaviors were observed in both control and vigilance period (VP) interactions, 13 behaviors were specific to controls, and 15 behaviors were specific to VPs.

ARs during both interaction types contained behaviors that involved direct contact of the AR performing gorilla with their partner. In controls, 11.0% (*n* = 25) of the performed behaviors involved contact with the partner (*allogroom*, *huddle*, *inspect*, *mouth*, *pull*, *push*, and *touch*) and 68.0% of these behaviors were performed while in a *sit* posture. Direct contact behaviors were observed in higher frequency (31.0%, *n* = 72) during VPs (*bite*, *block*, *drum*, *grab*, *hold*, *inspect*, *kick*, *pull*, *pull away*, *push*, and *touch*). Direct contact VPs were also mostly performed from a *sit* posture (78.9%).

Some behaviors in both control and VP ARs were highly visible or audible to the partner but did not involve engaging in direct contact with that partner. Again, these behaviors occurred in a higher frequency during VP ARs (27.3% of observed VP behaviors: *arm wave*, *chest-pound*, *gather hay*, *hand clap*, *hay display*, *headshake*, *pull hay away*, *reach*, *shake rope*, *tongue wag*, and *wall slap*) than during controls (4.8% of observed control behaviors: *adjust hay*, *arm swing*, *gather hay*, *hand clap*, and *throw*). Visible or audible behaviors performed by control gorillas were performed while *quadrupedal* (54.5%), *sitting* (27.3%), or *bipedal* (18.2%). The majority visible or audible VP behaviors were performed while *sitting* (60.0%); however, a *bipedal* posture was also frequently used (22.2%).

2.2.2.3. *Movements*

Control gorillas performed an AR most frequently while *moving away* (29.4% of observed movements, *n* = 28). VPs contained twice the number of observed movements than controls (*n* = 25), and VP gorillas performed an AR most frequently while *moving to* (29.1%, *n* =71) and *moving away* (25.8%, *n* = 63) from a partner (Fig. 49). Movements

could be further categorized to determine the types of movements that occurred when a gorilla performed an AR: 1) body movements that resulted in a postural adjustment; 2) movements that were directed toward a partner; 3) movements that were directed away from a partner; and 4) a movement pattern, e.g., a locomotive gait (Table 31). Control gorillas most frequently performed ARs while performing a movement that was directed away from the partner (48.4%, n = 46) or during a postural adjustment (35.8%, n = 34) [*partner-directed movement* = 15.8%, n = 15]. VP gorillas most frequently performed ARs accompanying a partner-directed movement (48.4%, n = 118) or a movement directed away from a partner (29.1%, n = 71) [*postural adjustment* = 18.4%, n = 45; *movement pattern* = 4.1%, n = 10; see Table 31].

Movements by control gorillas were most often observed with a *sit* (44.2%) and *quadrupedal* (42.1%) posture. Movements by VP gorillas were most often observed with a *quadrupedal* (42.6%) and *sit* (37.7%) posture, and the incidence of *bipedal* was twice as high in VPs (8.6%) than in controls.

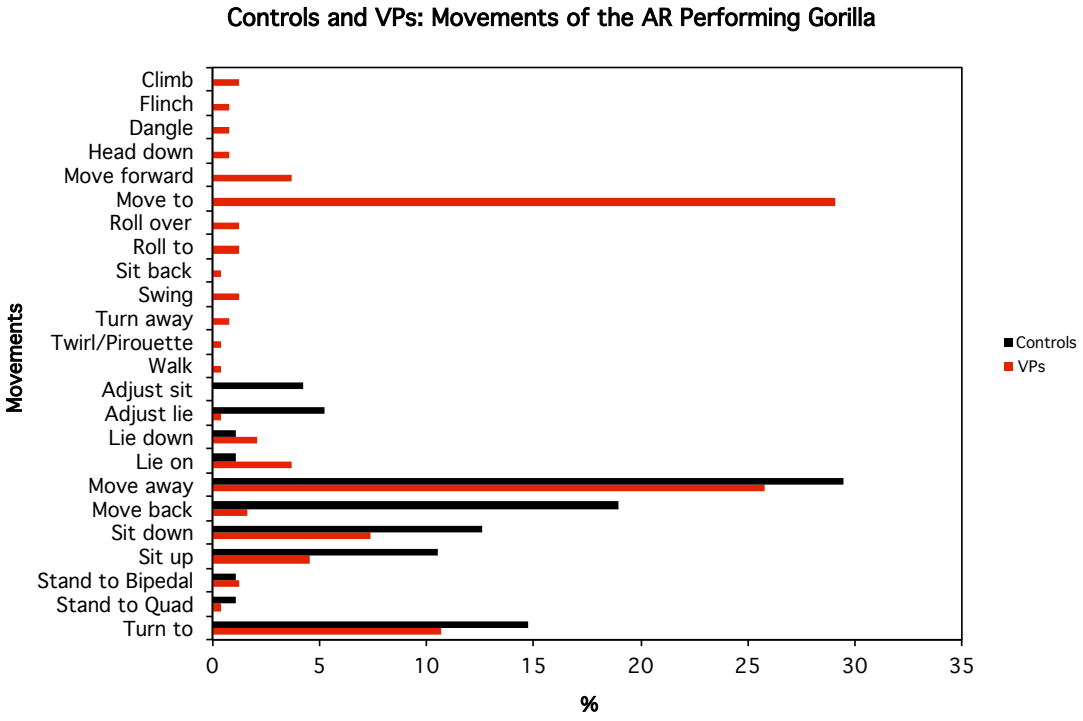


Fig. 49 - The movements of the gorilla that performed the attention realignment. Ten movements were observed in both control and vigilance periods (VPs), 1 movement was specific to controls, and 14 movements were specific to VPs.

	Movements	Controls (%)	Control *n*	VPs (%)	VP *n*
Postural adjustments	Adjust (x), head down, lie down, roll over, sit back, sit down, sit up, stand to bipedal, stand to quad	35.8	34	18.4	45
Partner directed	Lie on, move forward, move to, roll to, turn to	15.8	15	48.4	118
Partner opposite	Flinch, move away, move back, turn away	48.4	46	29.1	71
Movement pattern	Climb, dangle, swing, twirl/pirouette, walk	-	-	4.1	10

Table 31 – The types of movements performed by a gorilla that also performed an attention realignment.

2.2.2.4. *Monitoring*

In controls, a gorilla performed an AR to monitor a partner in 2 observations (in both, the partner *watched* the other partner's actions). VP gorillas performed an AR to *scan* the environment in 3 observations and *watched* a partner's action in remaining observations (85.0%; $n = 17$) [Table 32]. VP gorillas performed a monitoring AR from a *sit* posture in 95.0% of cases (*lie* = 5.0%).

Partner action(s)	% of monitoring actions observed
Eat	23.5
Gather hay	11.8
Hay display	5.9
Hand clap	17.6
Move away	11.8
Raise leg	5.9
Sit up	5.9
Stand to bipedal	11.8
Turn away	5.9

Table 32 – The proportions of the actions that were performed by the partner gorilla that a monitoring AR was directed toward.

2.2.3. Summary

With the exception of two instances, the gorilla that performed an AR also performed the actions that were observed. ARs during rest occurred significantly more in VPs than controls, and ARs between two resting gorillas also occurred significantly more in VPs. Nine behaviors were shared by both control and VP interactions, although the number of different behaviors was comparable between the interaction types (22 and 24, respectively). VP gorillas engaged in significantly more direct contact and audible/visible behaviors while performing an AR than controls.

Control gorillas performed ARs most frequently while performing *moving away* (29.4%)

or while engaged in a movement that was directed away from their partner (48.4%) or during a postural adjustment (35.8%). VP gorillas performed ARs while *moving to* (29.1%) or *moving away* (25.8%) from a partner or while engaged in movements that were partner-directed (48.4%) or directed away from a partner (29.1%). Overall, ARs in both interaction types appeared to accompany a variety of movements, regardless of the locomotive trajectory. Finally, monitoring was observed more frequently in VPs, particularly *watching* the actions of the partner, and gorillas engaged in monitoring primarily from a *sit* posture.

2.3. Gorilla dyads engaged in ARs: actions of the gorilla the AR was directed toward

This final section of the analyses investigated the actions of the gorilla partner that an AR was directed toward. In other words, when gorilla A performed an AR, what was gorilla B doing? Again, the subsets of 55 control and 301 VP interactions were analyzed, which resulted in the evaluation of 458 control and 1,018 VP ARs. A total of 478 control and 1,046 VP actions were analyzed (Table 33).

	Controls		**VPs**	
	n	**%**	***n***	**%**
a. Recipient of a partner behavior	-	-	4	0.4
b. Actor				
1. Inactive/Resting	147	30.7	609	58.2
2. Behaviors	232	48.5	190	18.2
3. Movement	95	19.9	245	23.4
4. Monitoring	4	0.8	2	0.2
Totals	**478**		**1,046**	

Table 33 – The counts (*n*) and corresponding proportions (%) of the actions that a gorilla performed when an AR was directed toward them.

2.3.1. Recipient of a partner behavior

There were no observations for control ARs where the gorilla that performed the AR also performed an action on their partner. There were only 4 ARs observed during VPs in which the gorilla that performed the AR also performed a direct action on their partner. The receiving partner gorilla in these cases, received both an AR and a direct action from the AR performing partner (*push*, *drum*, *grab arm* and *pull*, and *stand to bipedal* and *bite*). *Drum*, *grab arm* and *pull*, and *stand to bipedal* and *bite* were observed at the end of the VP.

2.3.2. Actor (gorilla performed an action)

2.3.2.1. *Inactive/Resting*

During controls, it was more frequent that an AR was directed toward a partner that was active (67.9%, n = 311) than inactive (32.1%, n = 147). Unlike controls, VP ARs were directed at a partner that was resting (59.6%, n = 609) more frequently than at a partner that was active (40.4%, n = 413). The direction of an AR toward a resting partner occurred more frequently during VPs than during controls. In both controls and VPs, an AR was most often directed toward a resting gorilla in a *sit* posture (controls = 67.3%; VPs = 69.9%); however, control ARs were also often directed toward a *lying* partner (18.4%), whereas VP ARs were directed toward a *quadrupedal* partner (20.5%).

2.3.2.2. *Behaviors*

The gorilla the AR was directed toward was observed to perform 23 behaviors during controls and 26 during VPs; 13 of these behaviors were present in both interaction types (Fig. 50). The gorilla partner that the AR was directed toward was most frequently

eating in both controls (64.2%) and VP interactions (42.4%).

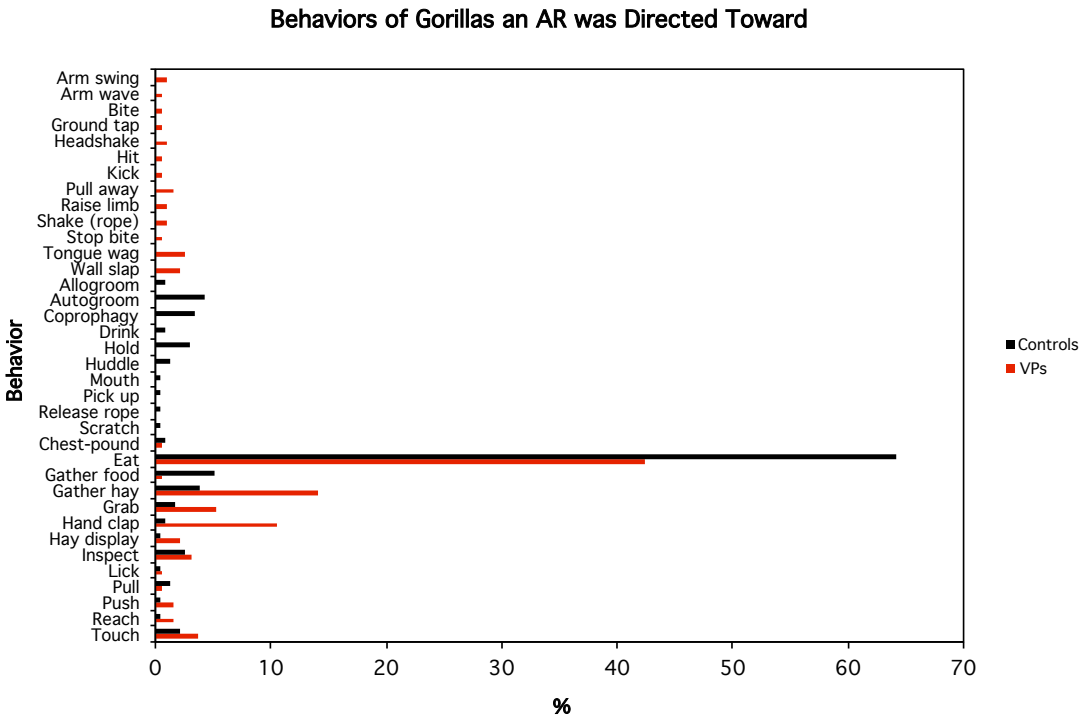


Fig. 50 – The proportions of behaviors performed by the gorilla that the attention realignment was directed toward. Thirteen behaviors were common to both controls and vigilance periods (VPs), 10 behaviors were specific to controls, and 13 behaviors were specific to VPs.

ARs in both controls and VPs were frequently directed toward behaviors that involved direct contact from the partner gorilla. In control interactions, 7.8% of the partner's performed behaviors (*n* = 26, *allogroom*, *grab*, *huddle*, *inspect*, *mouth*, *pull*, *push*, *scratch*, and *touch*) involved contact and 80.8% of these postures were performed by a *sitting* partner. More frequently than controls, VP ARs were directed toward a partner who was performing a direct contact behavior (17.8%, *n* = 39; *bite*, *grab*, *hit*, *inspect*, *kick*, *pull*, *pull away*, *push*, *stop bite* and *touch*), and similar to controls, the majority of these behaviors were performed by a partner in a *sitting* position (74.3%).

In some instances, the behaviors that were performed by the partner that the AR was directed toward were highly visible or audible but did not involve direct contact with the partner. These behaviors were observed more frequently during VP ARs (38.7%, *n* = 67; behaviors: *arm swing*, *arm wave*, *chest-pound*, *gather food/hay*, *ground tap*, *hand clap*, *hay display*, *headshake*, *raise limb*, *reach*, *shake rope*, *tongue wag*, and *wall slap*) than control ARs (11.2%, *n* = 26; behaviors: *chest-pound*, *gather food*, *gather hay*, *hand clap*, *hay display*, and *reach*). Audible/visible behaviors in controls were most frequently performed by a partner in a *quadrupedal* posture (76.9%), whereas VP audible/visible behaviors were performed in a variety of postures (*bipedal* = 14.9%; *hang* = 6.0%, *lie* = 20.9%; *quadrupedal* = 22.4%; *sit* = 35.8%).

2.3.2.3. *Movements*

Both control and VP gorillas directed an AR most frequently toward a partner gorilla that was *moving away* (*controls*: 30.5%, *n* = 29, *VPs*: 31.0%, *n* = 76) or *moving to* (*controls*: 25.3%, *n* = 24; *VPs*: 26.1%, *n* = 64). Again, VPs contained a higher number of types of movements than controls (*n* = 26; *controls*: *n* = 16) [Fig. 51]. ARs in both interaction types were most often directed toward a partner that was in a *quadrupedal* posture (controls = 48.4%; VPs = 50.8%), which corresponded to the high proportions of *move away* and *move to* movements observed in partner gorillas.

Movements could again be further categorized to determine the types of partner movements that an AR was directed toward: 1) body movements that resulted in partner postural adjustments; 2) movements that were directed toward the AR performing partner; 3) movements that were directed away from the AR performing partner; or 4) a

movement pattern (Table 34). Control gorillas directed an AR comparably toward a partner that directed their movement away (34.7%, *n* = 33), directed their movement toward (33.7%, *n* = 32) and performed a postural adjustment (29.5%, *n* = 28) [*movement pattern* = 2.1%, *n* = 2]. VP gorillas more frequently directed an AR toward a partner that performed a movement away (37.5%, *n* = 92) or a movement toward (35.1%, *n* = 86) [*postural adjustment* = 19.6%, *n* = 48; *movement pattern* = 7.7%, *n* = 19].

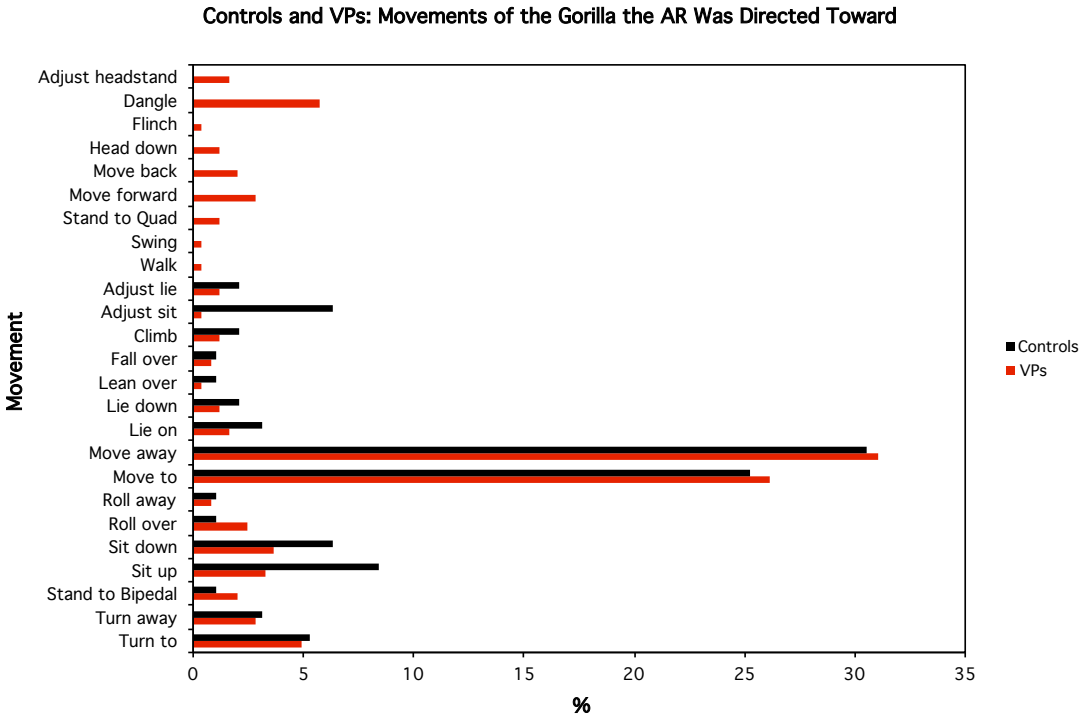


Fig. 51 – The movements of the partner gorilla that the attention realignment was directed toward. This graph illustrates the movements that partner gorillas performed during control and vigilance periods. *Move away* and *move to* were the most frequent movements observed in both interaction types.

	Movements	Controls (%)	Control *n*	VPs (%)	VP *n*
Postural adjustments	Adjust (x), fall over, head down, lean over, lie down, roll over, sit down, sit up, stand to bipedal, stand to quad	29.5	28	19.6	48
Partner directed	Lie on, move forward, move to, roll to, turn to	33.7	32	35.1	86
Partner opposite	Flinch, move away, move back, roll away, turn away	34.7	33	37.5	92
Movement pattern	Climb, dangle, swing, walk	2.1	2	7.7	19

Table 34 – The types of movements of the partner gorilla that an AR was directed toward.

2.3.2.4. *Monitoring*

During controls, 4 cases were observed where an AR was directed toward a partner that was performing a monitoring action. In 3 of these cases, an AR was directed toward a partner that was engaged in a *stare*. In the fourth observation, an AR was directed at a gorilla that *looked* up toward the enclosure ceiling. There were 2 observations during VPs where an AR was directed toward a partner that was performing a monitoring action. In the first case, an AR was directed toward a partner that was *watching* the AR partner. In the second case, an AR was directed at a partner that *looked* over their shoulder at the AR partner.

2.3.3. Summary

With the exception of 4 instances during VPs, the partner gorilla did not receive a simultaneous AR and action. In controls, ARs were frequently directed toward an active partner, whereas VP ARs were significantly directed toward a resting partner. Controls

and VPs had comparable amounts of behavior types and 13 behaviors spanned both interaction contexts. In comparison to controls, ARs during VPs were significantly directed toward a *sitting* partner that was in direct contact or a partner that performed an audible/visible behavior in a *sitting* posture.

In both controls and VPs, ARs were most frequently directed toward a partner that was performing *moving away* or *moving to* movements from a *quadrupedal* posture. Control ARs were comparably directed toward a partner that was performing a movement toward, away, or a postural adjustment. VP ARs were most frequently directed toward a partner that was performing a movement toward or away; together, these results indicate that ARs in both interaction types appear to be directed toward partner movements in general, regardless of the locomotive trajectory. Finally, ARs were infrequently directed toward a partner that was engaged in a monitoring action.

Discussion

The aim of this study was to complement the attentional cue analyses of Chapter 4 and to further investigate the postures, behaviors, and movement of gorilla dyads in control and VP interactions with variable amounts of attentional changes. As discussed in Chapter 4, gauging the direction of attention and maintaining an awareness of a partner's attentional state are crucial components leading to the continuation or termination of gorilla play. For the gorilla social dyad, attentional cues have the ability to regulate a social interaction through the conveyance of socially relevant information, which can frame the ensuing behavioral context. This information is useful for the immediate context – indicating "not right now" and "now" – and also in preparation for a subsequent interaction. During

social interactions, the changes in corporal cues and the physical actions that gorillas engage in also impact the dynamic social relationship between the partners. Postures, behaviors, and movements not only provide information about the overall social context of an interaction, e.g., is it playful?, but can emphasize and aid in the direction of an interaction toward a partner when accompanied by corresponding changes in partner-directed attention.

1. Gorilla postures

The general analysis of postures demonstrated that overall, *lie*, *quadrupedal*, and *sitting* postures were present consistently in both control and VP interactions, regardless of the attention changes that occurred. This comparability in postural use and frequency indicates that the postures examined in this study are common components of the gorilla repertoire and are not context specific. Although some postures (*crouch* and *headstand*) were exclusive to VPs and gorillas had a tendency to use *bipedal* and *hang* postures more frequently during VPs, their overall minimal occurrence within VPs does not indicate that they are reliable indicators of play.

However, it can be suggested that some postures in both interaction types are residual from or a product of a preceding action. Particularly for VPs, the last action of play may create a continuity of posturing between the play period and VP. Gorillas that are engaged in seated, close contact rough-and-tumble play may also remain in the seated posture when they break from play. For example, the slight increase in the prevalence of bipedalism may have been the result of the surrounding playful context of VPs. The gorillas were often observed to engage in bipedal wrestling during play (*personal*

observation), and a bipedal stance is a common mammalian play-fighting posture that frees the hands for direct interaction with the partner and a variety of playful behaviors (*Ursus americanus*: Henry & Herrero, 1974; *Gorilla gorilla*: Tanner & Byrne, 1996, 2010; *Suricata suricatta*: Wemmer & Fleming; 1974). The exaggeration and capriciousness of behaviors (one of the hallmarks of play behavior) that occurred during the play period, may have carried across the VP boundary and created a sustained playful context for the VP, thus influencing any subsequent posturing. The use of an exaggerated body posture during a VP, such as a *headstand* or *bipedal*, could work to reaffirm the playful context and indicate to a partner an eagerness to resume play. However, the majority of VPs in this study were followed by a resumption in play; therefore, correlations between exaggerated posturing and the frequency of play resumption could not be reliably examined.

2. Resting vs. active gorillas

In controls, an active gorilla typically performed an AR (65.1%), and an AR was also typically directed toward a gorilla that was active (69.3%). This differed significantly from VPs in which an AR performing gorilla was typically a resting gorilla (54.6%) and an AR was typically directed toward a resting gorilla (58.2%). The differences in activity levels between control and VP gorillas can be potentially explained by the contextual difference between VPs and controls. VPs were physical breaks embedded between play periods and reflected a temporary recess from an immediately previous and highly energetic social interaction. Chapter 4 emphasized that the frequent attentional exchanges between VP gorillas indicate that VPs are not periods of disengagement between play partners. Similarly, this higher "resting" in VPs does not reflect

disengagement between partners, but instead indicates the occurrence of a physical rest from play, which allows the gorillas to take a *physical* break but not an *attentional* break from the play interaction. VP resting may therefore serve two functions for juvenile gorillas: 1) an immediate function that provides the gorillas with physical rest from the physical exercise of play, and 2) a long-term function that allows gorillas to learn about the attentional and behavioral cues of a partner. While a physical resting of the body may occur during a VP, continued attentional behaviors would offer a method of maintaining social engagement with a partner, which would be particularly useful for eventual play resumption.

However, controls were non-playful, neutral scenarios; this operational composition of controls (i.e., interactions that lacked energetic social interactions between gorillas) may have contributed to the lower amount of observed resting because control gorillas were often engaged in neutral diurnal activities (e.g., eating). Arguably, the frequent control ARs could be explained as a by-product of activity rather than fulfilling a socially communicative function; where there is an increase in activity, there is also an increase in the likelihood of accidentally provoking or performing an AR in relationship to a group mate.

3. Behaviors

In comparison to controls, VP gorillas exhibited a higher variability of behaviors that represented three modalities – direct contact (tactile), auditory, and visual. Behaviors that were visible and/or audible in nature used either the self or an element of the environment to generate the visible or audible component. Behaviors of all three

modalities occurred significantly more during VPs than controls and occurred simultaneously with ARs that were either produced by or received from a partner. VPs also generated VP specific behaviors (e.g., *arm wave*, *bite*, *drum*, *grapple*, *ground tap*, *hand roll*, *headshake*, *hit*, *kick*, *raise limb*, *shake rope*, *slap*, *tongue wag*, and *wall slap*).

The overall higher variability in direct contact, visible, and audible behaviors in VPs suggests that the diversity in the gorilla behavioral repertoire may relate to the contextual differences between controls and VPs, i.e., play versus non-play. Just as the gorilla behavioral repertoire can be extensive (see the GBAG ethogram collection, Ogden *et al*., 1991), the gorilla play behavior repertoire can also be quite large, particularly because a number of behaviors derive from other social contexts, e.g., aggression. Gestural studies have shown that high amounts of behaviors and gestures occur within the context of primate play and are used flexibly (*gorillas*: Genty & Byrne, 2009; Genty *et al.*, 2009; Pika *et al*., 2003). This is also well-documented within the play-fighting literature, in which the behaviors used within an aggressive context are structurally or temporally modified by the participants for the inclusion in this arena of play (Pellis & Pellis, 1996, 2009). For example, the direct contact behavior *bite* can inflict serious damage when used as aggression; however, the use of *bite* is a common play behavior and is typically modified in either its physical application on a partner, i.e., the strength of the bite or the degree in which the teeth/lips are used, or in its placement on a partner's body, i.e., the species-typical play target of the shoulder (Burghardt, 2005; Palagi & Cordoni, 2009; Pellis, 1997; Pellis & Pellis, 1996, 2009). Another audible/visible example, the *chest-pound*, is used by adult gorillas as an agonistic threat but is frequently performed by

juvenile gorillas before and during social play (Brown, 1988; Schaller, 1963).

Why are behaviors also accompanied by ARs? One possibility is that changes in attention orientations are a consequence of directing any behavior toward a partner. Behaviors that involve direct contact between partners may require a simultaneous attentional orientation toward the partner to guide the gorilla's behavior to a specific target. For example, to grab a partner's arm, the grabbing gorilla's body must be, to some degree, oriented toward the partner. To increase the efficiency in grabbing a partner's arm, the gorilla must know where the arm is and would need to gather this information visually, i.e., a targeted orientation of the head and/or the eyes. In VP interactions with 0-1 AT, direct contact behaviors occurred when a gorilla was either already oriented toward their partner (52.3% of direct contact behaviors) or they oriented themselves toward their partner (34.1%) and performed the behavior. However, because of the study design and data collecting procedure, all direct contact behaviors that were evaluated during interactions containing ARs naturally occurred with an AR. While these results suggest that there is a tendency for gorillas to be oriented toward their partner when performing a direct contact behavior, the scope of this study can only suggest that this is a trend, and further empirical evidence that investigates direct contact and changes in attention orientation is necessary.

The results for audible/visible behaviors suggest a similar tendency for gorillas to orient their attention toward a partner when performing an audible/visible behavior, and these types of behaviors appear to attract the attention of a partner. In VP interactions with 0-1

AT, the gorillas performed an audible/visible behavior when they were either already oriented toward their partner (76.9%) or with an orientation toward their partner (23.1%). However, as was mentioned above, the data collection procedure only evaluated audible/visible behaviors that occurred with an AR, and the scope of this study can only suggest that this partner-directed orientation is a trend that requires further empirical evidence to specifically investigate these types of behaviors and their corresponding attention orientations. Nonetheless, it can be speculated that ARs may also serve an additional communicative function. Communication through visual or audible behaviors would be more explicit when the attention of the performing gorilla is focused on the desired partner. For instance, a handclap that is performed by a gorilla that is oriented toward their partner holds a different social meaning than a handclap that is performed while the gorilla's attention is oriented toward the floor. This is also communicatively relevant for a recipient gorilla; a targeted handclap can only be communicative if the target is attending. Direct contact behaviors can also serve a communicative function; although the directionality of the behavior may be implicit in the tactile nature of the behavior itself, the accompaniment of a partner-directed attention orientation might simply reaffirm that the behavior being performed is directed specifically at that partner. Therefore, the orientation of attention in combination with a performed or received behavior impacts the overall communicative message.

Within VPs, the presence of ARs in combination with performed and received behaviors emphasizes that attentional orientation is an integral component of these particular gorilla social interactions. Previous evaluations of gestural and intentional communication in the

play context have shown that great apes use behaviors flexibly, intentionally, and alter gestural modality in response to the attentional state of the partner, e.g., juvenile chimpanzees solicit play with an arm-raise, a visual signal, only when the partner has an appropriate attentional orientation (*gorillas*: Genty *et al*., 2009; Tanner & Byrne, 1996; *chimpanzees*: Tomasello *et al*., 1994). The extent in which VP gorillas modify behavior modality in response to partner attentional orientation was however, outside the scope of this thesis. In relationship to behavioral exchanges between play partners, this study can only suggest that gorillas tend to direct their attention along with, or focus their attention on behaviors that occur during VPs. Future play research would benefit from a fine-grain analysis of VP gestural sequences to determine how concurrent gestures and attention orientations modify gorilla VP behaviors and whether there is any influence on the resumption of play between the partners.

4. Movement

VP gorillas performed ARs most frequently while *moving to* a partner and performed the most ARs in conjunction with partner-directed movements (e.g., *move forward*, *move to*, *roll to*, and *turn to*). This consistent orientation between ARs and partner-directed movements is likely a result of the gorilla's direction of movement. It stands to reason that a gorilla performed an AR simultaneously with a partner-directed movement because their attention alignment and locomotion trajectory were inevitably congruent with one another. It was not observed that a gorilla that moved toward their partner with their eyes, head, and body oriented away (although atypical movements are certainly possible, especially during play).

Interestingly though, ARs were also frequently performed by a gorilla that was simultaneously *moving away*, and this occurred during both controls and VPs. Although the gorilla's locomotion trajectory was headed away from a partner, shifts of attention in some form, either eye, head, or body, were realigned back in the direction of the partner. The occurrence of this pattern in both controls and VPs suggests that some form of attentional orientation directed toward a partner while engaged in away locomotion is not context specific, and rather, occurs in locomoting gorillas in general, at least in the reduced space of a captive enclosure.

Similarly, both control and VP gorillas frequently directed ARs toward a partner that was *moving to* or *moving away* from them, which suggests that gorillas realign their attention toward a locomoting partner in general, regardless of the movement trajectory. One explanation for this is that locomotion in general may trigger social monitoring by conspecifics as an overall attention-related feature of gorilla society. In this sense, the movements of group mates draw attentional interest and have the potential to generate social interactions, and thus, gorillas remain attentive to this possibility when they are performing a movement or when a group mate is moving. Regardless of context, attentiveness to moving group mates would be socially informative concerning the spatial distribution of conspecifics and the relationships of conspecifics to important environmental elements, e.g., food locations, optimal resting locations, current and impending social interactions, etc. VP gorillas would gain additional play-specific information, which would be necessary for the reengagement or termination of play. ARs directed toward a moving play partner would be informative about the trajectory of

the partner's locomotion, e.g., are they approaching or are they leaving? Similarly, a moving gorilla that directs an AR toward a partner would obtain information about the partner's direction of attention and actions, e.g., does the partner see the movement and are they responding to it? In either instance, orienting attentional cues toward VP movements would be a worthwhile strategy for play partners because the direction of a moving partner, either toward or away, can quickly affect the reengagement or termination of play.

5. Conclusions

The frequent occurrence of changes in attention orientations by both gorilla partners during controls and VPs indicates that overall, gorillas appear to be attentive to the behaviors and movements of proximal conspecifics and make frequent adjustments to their attention orientations in relationship to their own activity and the activity of a partner. VP interactions contained a higher variability in behaviors and movements than controls, which is most likely related to the surrounding play context. A high incidence of resting was also associated with ARs, which further emphasizes the attentional results of Chapter 4, and highlights that while VPs may offer the opportunity for physical rest between playing gorillas, they are not periods of disengagement between partners. Instead, the gorilla partners remain attentionally active and engaged with their play partner even if no explicit activity is taking place. The analyses of performed and received behaviors indicates that direct contact and audible/visible behaviors occur significantly more in VPs than in controls, and there is a tendency for these types of behaviors to co-occur with partner-directed attention. Additionally, the observation that movement frequently co-occurs with partner-directed attention suggests that movements

in general, appear to generate social monitoring between gorillas.

Overall, it can be proposed that VPs serve multiple roles for socially playing gorillas: 1) VPs offer physical rest for play engaged gorillas, while maintaining attentional engagement; 2) VPs offer the opportunity to assemble socially relevant information about the behaviors, movements, and attentional directions of the play partner; 3) through the use of and interaction between ARs, behaviors, movements, and postures, VPs can impart willingness and receptivity (or lack thereof) to reengage in play behavior; and 4) within the boundaries of play, VPs offer an arena for gorillas to rehearse and refine the interpretation and delivery of attentional cues.

CHAPTER 6:

General Discussion

Chapter 6: General Discussion

"You can discover more about a person in one hour of play than in a year of conversation." – Plato

The overall aim of the studies contained within this thesis was to expand on the current research relative to the adaptive use of attention cues in non-human primates and their role in the play behavior of lowland gorillas. The studies presented are of two types: experimental, to explore the role of changes in eye morphology in the evolution of attentional cueing; and observational, to contribute to the understanding of the general social cues used by gorillas to gauge the attention and receptivity of playmates to maintain or terminate play during so-called vigilance periods. This experimental research was guided by previously posited primate gaze hypotheses – the *gaze camouflage hypothesis* (Kobayashi & Kohshima, 2001) and *cooperative eye hypothesis* (Tomasello *et al.*, 2007) – and evaluated the claims presented by the study authors as they pertained to the design of cues and the cue values of apes with dark and white sclera. To date, little research had been conducted on the actual signaling value of eyes with white sclera, the acquisition and development of gorilla social cognitive abilities through play behavior, or the general utilization of attention cues in the play context. This thesis was first a specific examination of the information contained within the eye gaze cue (Chapters 2 and 3) with particular emphasis placed on the influence of a white sclera morphological variation. The scope of the thesis was then broadened in Chapters 4 and 5 to address the application of the eye gaze cue and other general attention cues, such as head and body orientations, within the specific behavioral context of play.

Overview of the studies

Chapter 1

Chapter 1 of this thesis presented a general overview of the gaze mechanisms (Baron-Cohen, 1994; Perrett & Emery, 1994; Perrett *et al.*, 1985) involved in gaze-following and mutual attention. Available gaze information suited for great ape gaze-following (Bräuer *et al.*, 2005; Tomasello *et al*., 1998) and the interpretation of conspecific attentional states was also addressed (Liebal *et al*., 2004; Leavens *et al*., 2009; Pika *et al*., 2003; Poss *et al*., 2006), highlighting the conflicting literature on great ape sensitivity to eye gaze versus head and body orientations. Play behavior was introduced as an optimal arena to examine how gorillas use and practice conveying and interpreting social information via general attention cues.

Chapter 2

The analyses of Chapter 2 expanded on the primate eye coloration and morphological survey of Kobayashi and Kohshima (2001) in multiple ways: 1) this study included an increased gorilla sample size for width/height ratio (WHR – measure of the elongation of the eye) and exposed sclera size (SSI) quantitative analyses; 2) introduced novel WHR and SSI species comparisons between lowland gorillas (*Gorilla gorilla*), mountain gorillas (*Gorilla beringei*), and humans; 3) introduced species comparisons between averted and direct gazing eyes; and 4) introduced a novel qualification of pigment degradation patterns in gorilla sclera to evaluate the presence of a white sclera characteristic.

The direct gaze results of Chapter 2 differed from the original study's direct gaze results indicating that the human eye differs from the gorilla eye more importantly in its elongation than in the total amount of exposed sclera. Additionally, no differences were observed between humans and gorillas in the amount of exposed sclera in direct gazing eyes. Averted human and gorilla gazes also contained larger amounts of exposed sclera.

Chapter 2 documents for the first time the natural occurrence of a white sclera characteristic in gorillas (*Gorilla gorilla*) with up to 90% of the observed lowland gorilla specimens possessing some degree of depigmentation and approximately 12% of gorillas showing a complete white sclera in averted gazes. The observations of varying degrees of sclera depigmentation in gorillas demonstrate that what is widely accepted as a fact in the literature, namely that all the great apes present an all-dark sclera coloration scheme in their eyes, is not categorically accurate and may therefore contradict the gaze camouflage function proposed for all-dark ape eyes. These results also oppose a portion of the *cooperative eye hypothesis* (Tomasello *et al*., 2007) and further suggest that gorillas do not have dark sclera as an adaptation to camouflage gaze direction. The preservation of a white sclera in gorillas suggests that its presence may not confer significant disadvantages to gorillas; however, the lack of preferential selection suggests that a white sclera does not confer any significant advantages either. Chapter 2 acknowledges sclera variability in gorillas, and the subsequent chapters address its potential contribution to gaze direction judgments and its general use within the socially important context of play.

Chapter 3

Chapter 3 of this thesis takes advantage of the naturally occurring white sclera variation described in the previous chapter and explores the contribution of white and dark sclera to available directional gaze information in the isolated regions of human and great ape eyes as perceived by human observers. This chapter used the "Bogart illusion" (Sinha, 2000) and polarity contrast cues to investigate the perception of gaze direction in naturalistic examples of dark and light sclera great apes and humans.

The results of Chapter 3 indicated that human observers are proficient at determining gaze direction in dark sclera ape eyes; however, the speed and accuracy of gaze direction judgments were enhanced (in both human and great ape eyes) when white sclera was available. These results provide partial support for the *cooperative eye hypothesis* (Tomasello *et al.*, 2007), in that a light sclera adaptation, regardless of human or ape source, would have been beneficial for joint attentional interactions that relied on eye gaze direction judgments, at least from the perspective of modern humans. However, the human capacity to determine gaze direction in dark sclera eyes indicates that: 1) human gaze capabilities can be flexibly employed for a number of cues or cue constellations and do not rely on a single gaze cue, e.g., a polarity contrast; and 2) dark sclera great ape eyes contain sufficient gaze information for a human observer to determine gaze direction, which indicates that while a light/dark contrast certainly enhances the presence of gaze direction information, its presence is not a necessary stipulation for the interpretation of gaze direction in other individuals.

The results of Chapter 3 in conjunction with the results of Chapter 2, suggest that the elongation of the human eye relative to the ape eye might have been a more important adaptive change in the evolution of the human eye. Specifically, this morphological change would have been significant in interactions that rely on direct gazes between individuals, e.g., communication, which could have affected the selection for highly visible eyes. Although the horizontal elongation of the human eye was not accompanied by a significant increase in the amount of exposed sclera for direct gazes, it is arguable that this elongation was accompanied by a white sclera adaptation to enhance iris contrast and further facilitate direct gaze communicative functions.

Chapter 4

The practical application and use of relevant attentional cues, including eye gaze but also more general cues such as head and body direction, within social interactions were the remaining objectives of both Chapters 4 and 5. Behavioral observations of captive western lowland gorillas (*Gorilla gorilla gorilla*) were used to further explore the use of general attentional cues of eye gaze, head orientation, and body orientation between gorilla partners within the dynamic context of play. A novel play component was defined and explicitly described, "vigilance periods", as the main period for behavioral observation within play bouts. These time intervals, where play had temporarily paused, offered a unique setting for the exploration of general cues of attention. VPs were compared to non-play restful control interactions to explore the similarities and differences in attentional cue use throughout interactions with differing social contexts.

Chapter 4 observed that 1) the majority of VPs contained one or more change in attention

orientation; 2) attentional realignments (ARs) occurred in higher densities in VPs than in controls; 3) in controls, a partner-directed body, head, or eye orientation was variable throughout interactions; 4) both body and head orientations were frequently oriented toward the partner throughout VPs and the congruency of direction between these two cues was high; and 5) when visible, VP eye gaze was often oriented away from the partner but became partner-directed as the VP approached termination.

The frequent redirection of an attentional cue in the direction of the play partner may serve the functions of both assembling and communicating social information, which would be advantageous for both the realigning gorilla and their partner. The increase in an attending eye gaze together with a consistent attending head orientation suggests that partner monitoring increased as the VP ended. The assembly of social information about a play partner through the frequent monitoring of the partner's actions and attentional state provides immediate information about the continued contextual state of the interaction. Similarly, a consistent body orientation toward a partner throughout the VP may be a cue of social receptiveness and willingness to continue play at a later time, but an averted eye gaze may emphasize "not right now". The trend of partner-directed eye gaze orientation as the VP ended would be a cue indicating preparedness, or a "now" cue, for reengagement.

In general, Chapter 4 indicates that attention cues may be used differently in the VP context than in non-play resting controls, and the high frequencies of changes in attention cue orientations indicates that gorilla partners are not socially disengaged. Thus far, VPs

have yet to be explored as a play component, but this study offers that VPs may be important to play because they represent an arena for gorillas to learn general social cognitive cues that can regulate social interactions.

Chapter 5

Overall, the analyses of attentional cue orientations in Chapter 4 suggested that cue orientations might provide a great deal of socially relevant information for conspecifics. Play researchers have previously emphasized that the examination of play and its defining attributes is a complex, multi-faceted study (Burghardt, 2005), and the specific evaluation of one of its elements typically leads to a discussion about several of its characteristics based on the intertwined nature of the many components of play. In this regard, Chapter 5 was a series of analyses of the attentional "engagement" observed in Chapter 4 to determine the relationships between these frequent changes in attention and changes in particular postures, behaviors, and movements.

The results of Chapter 5 indicated that in both controls and VPs, gorillas appear to be attentive to the behaviors and movements of proximal conspecifics and make frequent adjustments to their attention orientations in relationship to their own activity and the activity of their partner. In comparison to controls, VPs contained a higher variability and prevalence of behaviors (particularly behaviors involving direct contact or audible/visible components) and locomotive movements, and there was a tendency for these behaviors and movements to co-occur with partner-directed attention. The observation that movement frequently co-occurs with partner-directed attention suggests that movements in general appear to generate social monitoring between gorillas. VPs

were also associated with a higher incidence of resting gorillas, which emphasizes that VPs offer periods of *physical* rest but not *attentional* rest between partners.

Conclusions

This thesis focused on the specific attributes of attentional cues utilized by gorillas; it began with the availability of gaze-related information in great ape eye gaze and developed into a broader evaluation of eye gaze and other general attention cues as they relate to and are used within the developmentally important social context of play.

Chapter 2 emphasizes that the elongation of the human eye, rather than its sclera coloration, is the unique factor that may have driven selection for modern human eyes. This elongation parameter and the novel consideration of a white sclera morphology in the great apes challenges the current *gaze camouflage hypothesis* for all-dark great ape eyes, and the incorporation of this variability into future morphological studies of eye gaze and attention should be emphasized. Additionally, the contribution of a white sclera characteristic to the speed and accuracy of gaze direction judgments by human observers partially supports the *cooperative eye hypothesis*; however, a white sclera merely adds to the presently efficient gaze cues that are available in the eye region of ape faces. Whether a white sclera characteristic is also beneficial to great ape quick and accurate gaze direction judgments remains to be studied. Future research would benefit from the adaptation of the studies of Chapter 3 to incorporate great ape participants for a complete evaluation of white and dark sclera contributions on gaze direction judgments.

Although it has yet to be determined whether gorillas have varied gaze judgment skills

because of conspecific sclera variability, general attention cues are used within social interactions, and the repeated exposure to general attention cues throughout social play and the benign and relatively safe nature of the play context, appears to lend itself favorably for gorillas to rehearse and refine the interpretation and delivery of attentional cues. As special portions of play behavior, VPs differ from the non-play restful control context and serve multiple roles for gorillas engaged in social play: 1) VPs offer physical rest while attention remains engaged between play partners; 2) differences in attention cue orientation trends between VPs and control interactions suggest that attention might be used differently in VPs; 3) socially relevant information about the behaviors, movements, and attentional directions of the play partner can be assembled through VPs; and 4) VPs consist of a complex interaction of ARs, behaviors, movements, and postures that can be informative to an attentive partner regarding a willingness and receptivity (or lack of) to reengage in play. Therefore, I believe that VPs are an ideal arena for the further study of great ape general attention cues, as VPs represent a crucial portion of play, which is vital for the rehearsal and refinement of the attentional cues necessary for gorilla socio-cognitive development. Future play behavior research should accordingly incorporate VPs to generate a rich understanding of both the structure and the dynamics of play behavior in the development of cross-contextual great ape socio-cognitive abilities.

References

Adachi, I., Chou, D. P., & Hampton, R. R. (2009). Thatcher effect in monkeys demonstrates conservation of face perception across primates. *Current Biology, 19*, 1270-1273.

Adam, J. J., Paas, F. G. W. C., Buekers, M. J., Wuyts, I. J., Spijkers, W. A. C., & Wallmeyer, P. (1999). Gender differences in choice reaction time: evidence for differential strategies. *Ergonomics, 42*(2), 327-335.

Akhtar, N., & Gernsbacher, M. A. (2008). On privileging the role of gaze in infant social cognition. *Child Development Perspectives, 2*(2), 59-65.

Allen, C., & Bekoff, M. (2005). Animal play and the evolution of morality: an ethological approach. *Topoi, 24*, 125-135.

Alley, T. R. (1980). Infantile colouration as an elicitor of caretaking behaviour in Old World primates. *Primates, 21*(3), 416-429.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*, 227-267.

Amici, F., Aureli, F., Visalberghi, E., & Call, J. (2009). Spider monkeys (*Ateles geoffroyi*) and capuchin monkeys (*Cebus apella*) follow gaze around barriers: evidence for perspective taking? *Journal of Comparative Psychology, 123*(4), 368-374.

Ando, S. (2002). Luminance-induced shift in the apparent direction of gaze. *Perception, 31*, 657-674.

Ando, S. (2004). Perception of gaze direction based on luminance ratio. *Perception, 33*, 1173-1184.

Angantyr, M., Eklund, J., & Hansen, E. M. (2011). A comparison of empathy for humans and empathy for animals. *Anthrozoos, 24*(4), 369-377.

Ankel-Simons, F., & Rasmussen, D. T. (2008). Diurnality, nocturnality, and the evolution of primate visual systems. *Yearbook of Physical Anthropology, 51*, 100-117.

Anstis, S. M., Mayhew, J. W., & Morley, T. (1969). The perception of where a face or television 'portrait' is looking. *The American Journal of Psychology, 82*(4), 474-489.

Aureli, F., & Whiten, A. (2003). Emotions and behavioral flexibility. In D. Maestripieri (Ed.), *Primate Psychology* (pp. 289-323). Cambridge: Harvard University Press.

Baldwin, J. D., & Baldwin, J. I. (1973). The role of play in social organization: comparative observations on squirrel monkeys (*Saimiri*). *Primates, 14*(4), 369-381.

Baldwin, J. D., & Baldwin, J. I. (1974). Exploration and social play in squirrel monkeys (*Saimiri*). *American Zoologist, 14*, 303-315.

Baldwin, J. D., & Baldwin, J. I. (1977). The role of learning phenomena in the ontogeny of exploration and play. In S. Chevalier-Skolnikoff & F. E. Poirier (Eds.), *Primate Bio-Social Development: Biological, Social, and Ecological Determinants* (pp. 343-406). New York: Garland Publishing, Inc.

Bard, K. A. (1992). Intentional behavior and intentional communication in young free-ranging orangutans. *Child Development, 63*(5), 1186-1197.

Bard, K. A., & Leavens, D. A. (2009). Socioemotional factors in the development of joint attention in human and ape infants. In L. Roska-Hardy (Ed.), *Learning from*

Animals? Examining the Nature of Human Uniqueness: Taylor & Francis.
Bard, K. A., Costall, A., Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2005). Group differences in the mutual gaze of chimpanzees (*Pan Troglodytes*). *Developmental Psychology, 41*(4), 616-624.
Baron-Cohen, S. (1997). How to build a baby that can read minds: cognitive mechanisms in mindreading. In S. Baron-Cohen (Ed.), *The Maladapted Mind: Classic Readings in Evolutionary Psychopathology* (pp. 207-241). East Sussex: Psychology Press.
Baron-Cohen, S. (2005). The empathizing system: a revision of the 1994 model of the mindreading system. In B. Ellis & D. Bjorklund (Eds.), *Origins of the Social Mind*: Guilford Publications, Inc.
Baron-Cohen, S., Wheelwright, S., & Jolliffe, T. (1997). Is there a "language of the eyes"? Evidence from normal adults and adults with Autism or Asperger Syndrome. *Visual Cognition, 4*(3), 311-331.
Barton, R. A. (1998). Visual specialization and brain evolution in primates. *Proceedings of the Royal Society of London B, 265*, 1933-1937.
Barton, R. A. (2006). Primate brain evolution: integrating comparative, neurophysiological, and ethological data. *Evolutionary Anthropology, 15*, 224-236.
Bateson, G. (1968). Redundancy and coding. In T. A. Sebeok (Ed.), *Animal Communication: Techniques of Study and Results of Research* (pp. 614-626). Bloomington: Indiana University Press.
Bekoff, M. (1972). The development of social interaction, play, and metacommunication in mammals: an ethological perspective. *The Quarterly Review of Biology, 47*(4), 412-434.
Bekoff, M. (1974). Social play and play-soliciting by infant canids. *American Zoologist, 14*(1), 323-340.
Bekoff, M. (1995). Play signals as punctuation: the structure of social play in canids. *Behaviour, 132*(5-6), 420-429.
Bekoff, M. (2000). Animal emotions: exploring passionate natures. *BioScience, 50*(10), 861-870.
Bekoff, M. (2004). Wild justice and fair play: cooperation, forgiveness, and morality in animals. *Biology and Philosophy, 19*, 489-520.
Bekoff, M., & Allen, C. (1997). Intentional communication and social play: how and why animals negotiate and agree to play. In M. Bekoff & J. A. Byers (Eds.), *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*. New York: Cambridge University Press.
Bekoff, M., & Allen, C. (2002). The evolution of social play: interdisciplinary analyses of cognitive processes. In M. Bekoff, C. Allen & G. M. Burghardt (Eds.), *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition* (pp. 429-435). Cambridge, Massachusetts: The MIT Press.
Bekoff, M., Allen, C., & Burghardt, G. M. (Eds.). (2002). *The cognitive animal: empirical and theoretical perspectives on animal cognition*. Boston: Massachusetts Institute of Technology.
Bekoff, M., & Byers, J. A. (Eds.). (1998). *Animal play: evolutionary, comparative, and ecological perspectives*. Cambridge: Cambridge University Press.

Berlyne, D. E. (1960). *Conflict, arousal, and curiosity*. New York: McGraw Hill.
Bethell, E. J., Vick, S.-J., & Bard, K. A. (2007). Measurement of eye-gaze in chimpanzees (*Pan troglodytes*). *American Journal of Primatology, 69*, 562-575.
Bickham, J. (2008). The whites of their eyes: the evolution of the distinctive sclera in humans. *Lambda Alpha Journal, 38*, 20-29.
Bockler, A., Knoblich, G., & Sebanz, N. (2011). Observing shared attention modulates gaze-following. *Cognition, 120*, 292-298.
Bradley, B. J., & Mundy, N. I. (2008). The primate palette: the evolution of primate coloration. *Evolutionary Anthropology, 17*, 97-111.
Bräuer, J., Call, J., & Tomasello, M. (2004). Visual perspective taking in dogs (*Canis familiaris*) in the presence of barriers. *Applied Animal Behaviour Science, 88*, 299-317.
Bräuer, J., Call, J., & Tomasello, M. (2005). All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology, 119*(2), 145-154.
Breed, M. D., & Moore, J. (2012). *Animal Behavior*. Burlington, MA: Academic Press.
Briffa, M., & Weiss, A. (2010). Animal personality. *Current Biology, 20*(21), R912.
Brown, S. G. (1988). Play behaviour in lowland gorillas: age differences, sex differences, and possible functions. *Primates, 29*(2), 219-228.
Bugnyar, T. (2007). An integrative approach to the study of 'theory-of-mind'-like abilities in ravens. *The Japanese Journal of Animal Psychology, 57*(1), 15-27.
Bugnyar, T., & Heinrich, B. (2005). Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings of the Royal Society of London B, 272*, 1641-1646.
Bugnyar, T., Stöwe, M., & Heinrich, B. (2004). Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society of London B, 271*, 1331-1336.
Burgdorf, J., Kroes, R. A., Beinfeld, M. C., Panksepp, J., & Moskal, J. R. (2010). Uncovering the molecular basis of positive affect using rough-and-tumble play in rats: a role for insulin-like growth factor I. *Neuroscience, 168*, 769-777.
Burgdorf, J., & Panksepp, J. (2006). The neurobiology of positive emotions. *Neuroscience and Biobehavioral Reviews, 30*, 173-187.
Burger, J., Gochfeld, M., & Murray, B. G. (1992). Risk discrimination of eye contact and directness of approach in black iguanas (*Ctenosaura similis*). *Journal of Comparative Psychology, 106*(1), 97-101.
Burghardt, G. M. (1984). On the origins of play. In P. K. Smith (Ed.), *Play in animals and humans* (pp. 5-41). Oxford: Basil Blackwell, Inc.
Burghardt, G. M. (1985). Animal awareness: current perceptions and historical perspective. *American Psychologist, 40*(8), 905-919.
Burghardt, G. M. (1998). The evolutionary origins of play revisited: lessons from turtles. In M. Bekoff & J. A. Byers (Eds.), *Animal Play: Evolutionary, Comparative, and Ecological Perspectives* (pp. 1-26). Cambridge: Cambridge University Press.
Burghardt, G. M. (2005). *The genesis of animal play: testing the limits*. Cambridge, Massachusetts: The MIT Press.
Burkart, J., & Heschl, A. (2006). Geometrical gaze-following in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology, 120*(2), 120-130.

Burnham, T., & Hare, B. (2007). Engineering human cooperation: does involuntary neural activation increase public goods contributions? *Human Nature, 18*, 88-108.

Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *The American Naturalist, 146*(1), 25-40.

Byrne, R. W. (2003). Animal communication: what makes a dog able to understand its master? *Current Biology, 13*, R347-R348.

Byrne, R. W., & Tanner, J. E. (2006). Gestural imitation by a gorilla: evidence and nature of the capacity. *International Journal of Psychology and Psychological Therapy, 6*(2), 215-231.

Call, J., Bräuer, J., Kaminski, J., & Tomasello, M. (2003). Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *Journal of Comparative Psychology, 117*(3), 257-263.

Caro, T. (2005). The adaptive significance of coloration in mammals. *BioScience, 55*(2), 125-136.

Caro, T. (2009). Contrasting coloration in terrestrial mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*, 537-548.

Cartmill, E. A., & Byrne, R. W. (2010). Semantics of primate gestures: intentional meanings of orangutan gestures. *Animal Cognition*.

Chalmers, N. (1984). Social play in monkeys: theories and data. In P. K. Smith (Ed.), *Play In Animals and Humans* (pp. 119-145). Oxford: Basil Blackwell, Inc.

Changizi, M. A., Zhang, Q., & Shimojo, S. (2006). Bare skin, blood and the evolution of primate colour vision. *Biology Letters, 2*(2), 217-221.

Charman, T., Baron-Cohen, S., Swettenham, J., Baird, G., Cox, A., & Drew, A. (2000). Testing joint attention, imitation, and play as infancy precursors to language and theory of mind. *Cognitive Development, 15*, 481-498.

Chevalier-Skolnikoff, S. (1970). The primate play face: A possible key to the determinants of evolution of play. *Rice University Studies, 60*, 9-29.

Chevalier-Skolnikoff, S. (1986). An exploration of the ontogeny of deception in human beings and nonhuman primates. In R. W. Mitchell & N. S. Thompson (Eds.), *Deception: perspectives on human and nonhuman deceit* (pp. 205-220). Albany: State University of New York Press.

Cline, M. G. (1967). The perception of where a person is looking. *The American Journal of Psychology, 80*(1), 41-50.

Collins, C. E., Hendrickson, A., & Kaas, J. H. (2005). Overview of the visual system of *Tarsius*. *The Anatomical Record Part A, 287A*, 1013-1025.

Coss, R. G. (1979). Delayed plasticity of an instinct: recognition and avoidance of 2 facing eyes by the jewel fish. *Developmental Psychobiology, 12*(4), 335-345.

Cranach, M. v., & Ellgring, J. H. (1973). Problems in the recognition of gaze direction. In M. V. Cranach & I. Vine (Eds.), *Social Communication and Movement: Studies of Interaction and Expression in Man and Chimpanzee* (pp. 419-443). New York: Academic Press.

Dahl, C. D., Logothetis, N. K., Bülthoff, H. H., & Wallraven, C. (2010). The Thatcher illusion in humans and monkeys. *Proceedings of the Royal Society of London B, 277*, 2973-2981.

Davila-Ross, M., Menzler, S., & Zimmermann, E. (2008). Rapid facial mimicry in orangutan play. *Biology Letters, 4*, 27-30.

de Sousa, A. A., Sherwood, C. C., Schleicher, A., Amunts, K., MacLeod, C. E., Hof, P. R., et al. (2010). Comparative cytoarchitectural analyses of striate and extrastriate areas in Hominoids. *Cerebral Cortex, 20*, 966-981.

de Waal, F. (2001). Pointing primates: sharing knowledge...without language. *The Chronicle of Higher Education*, *47*, B7-B9.

de Waal, F. B. M., Dindo, M., Freeman, C. A., & Hall, M. J. (2005). The monkey in the mirror: hardly a stranger. *Proceedings of the National Academy of Sciences of the United States of America, 102*(32), 11140-11147.

de Waal, F. B. M., & Yoshihara, D. (1983). Reconciliation and redirected affection in Rhesus monkeys. *Behaviour, 85*(3/4), 224-241.

Dennett, D. C., & Haugeland, J. C. (1987). Intentionality. Retrieved 21 January 2009, from Oxford University Press.

Der, G., & Deary, I. J. (2006). Age and sex differences in reaction time in adulthood: results from the United Kingdom health and lifestyle survey. *Psychology and Aging, 21*(1), 62-73.

Dominy, N. J., Ross, C. F., & Smith, T. D. (2004). Evolution of the special senses in primates: past, present, and future. *The Anatomical Record Part A, 281A*, 1078-1082.

Dubuc, B. (2002). The brain from top to bottom. Retrieved 2011: http://thebrain.mcgill.ca/flash/index_a.html

Dugatkin, L. A., & Bekoff, M. (2003). Play and the evolution of fairness: a game theory model. *Behavioral Processes, 60*, 209-214.

Eckhart, G., & Lanjouw, A. (2008). *Mountain gorillas: biology, conservation, and coexistence* (1st ed.). Baltimore: Johns Hopkins University.

Emery, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews, 24*, 581-604.

Emery, N. J., & Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. *Nature, 414*, 443-446.

Emery, N. J., Dally, J. M., & Clayton, N. S. (2004). Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Animal Cognition, 7*, 37-43.

Emery, N. J., Lorincz, E. N., Perrett, D. I., Oram, M. W., & Baker, C. I. (1997). Gaze-following and joint attention in Rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology, 111*(3), 286-293.

Evers, E., Vries, H. D., Spruijt, B. M., & Sterck, H. M. E. (2012). Look before you leap - individual variation in social vigilance shapes socio-spatial group properties in an agent-based model. *Behavioral Ecology and Sociobiology*.

Fagen, R. (1981). *Animal play behaviour*. New York: Oxford University Press.

Fagen, R. (1984). Play and behavioural flexibility. In P. K. Smith (Ed.), *Play In Animals and Humans* (pp. 159-173). Oxford: Basil Blackwell, Inc.

Fagen, R. (1993). Primate juveniles and primate play. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile Primates: Life History, Development, and Behavior*. New York: Oxford University Press.

Farroni, T., Csibra, G., Simion, F., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proceedings of the National Academy of Sciences of the United States of America, 99*(14), 9602-9605.

Farroni, T., Johnson, M. H., Menon, E., Zulian, L., Faraguna, D., & Csibra, G. (2005). Newborns' preference for face-relevant stimuli: Effects of contrast polarity. *PNAS, 102*(47), 17245-17250.

Fay, M. J. (1989). Hand-clapping in western lowland gorillas. *Mammalia, 53*(3), 457-458.

Feng, W., Luo, W., Liao, Y., Wang, N., Gan, T., & Luo, Y.-J. (2009). Human brain responsivity to different intensities of masked fearful eye whites: An ERP study. *Brain Research, 286*, 147-154.

Ferrari, P. F., Kohler, E., Fogassi, L., & Gallese, V. (2000). The ability to follow eye gaze and its emergence during development in macaque monkeys. *Proceedings of the National Academy of Sciences of the United States of America, 97*(25), 13997-14002.

Fitch, W. T., Huber, L., & Bugnyar, T. (2010). Social cognition and the evolution of language: constructing cognitive phylogenies. *Neuron, 65*, 795-814.

Flack, J. C., Jeannotte, L. A., & de Waal, F. B. M. (2004). Play signaling and the perception of social rules by juvenile chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 118*(2), 149-159.

Fletcher, A. W. (2006). Clapping in chimpanzees: evidence of exclusive hand preference in a spontaneous, bimanual gesture. *American Journal of Primatology, 68*, 1081-1088.

Fontaine, R. P. (1994). Play as physical flexibility training in five ceboid primates. *Journal of Comparative Psychology, 108*(3), 203-212.

Forrester, G. S. (2008). A multidimensional approach to investigations of behaviour: revealing structure in animal communication signals. *Animal Behaviour, 76*, 1749-1760.

Fossey, D. (1979). Development of the mountain gorilla (*Gorilla gorilla beringei*): the first thirty-six months. In D. A. Hamburg & E. R. McCown (Eds.), *The Great Apes* (pp. 138-184). London: The Benjamin/Cummings Publishing Company.

Fox, M. W. (1976). Inter-species interaction differences in play actions in canids. *Applied Animal Ethology, 2*, 181-185.

Friesen, C. K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychonomic Bulletin & Review, 5*(3), 490-495.

Gácsi, M., Miklósi, A., Varga, O., Topál, J., & Csányi, V. (2004). Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Animal Cognition, 7*, 144-153.

Galef, B. G. (1995). Why behaviour patterns that animals learn socially are locally adaptive. *Animal Behaviour, 49*, 1325-1334.

Gallese, V. (2003). The manifold nature of interpersonal relations: the quest for a common mechanism. *Philosophical Transactions of the Royal Society of London, Biological Sciences, 358*, 517-528.

Gaunet, F., & Deputte, B. L. (2011). Functionally referential and intentional communication in the domestic dog: effects of spatial and social contexts. *Animal Cognition*, *14*(6), 849-860.

Gentry, R. L. (1974). The development of social behavior through play in the Steller sea lion. *American Zoologist, 14*(1), 391-403.

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of

the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Animal Cognition, 12*, 527-546.

Genty, E., & Byrne, R. W. (2010). Why do gorillas make sequences of gestures? *Animal Cognition*, *13*(2), 287-301.

Gerald, M. S., Waitt, C., & Maestripieri, D. (2006). An experimental examination of female responses to infant face coloration in rhesus macaques. *Behavioral Processes, 73*, 253-256.

Gibson, J. J., & Pick, A. D. (1963). Perception of another person's looking behavior. *The American Journal of Psychology, 76*(3), 386-394.

Gillespie, D. L., & Leffler, A. (1983). Theories of nonverbal behavior: A critical review of proxemics research. *Sociological Theory, 1*, 120-154.

Gómez, J.-C. (1990). The emergence of intentional communication as a problem-solving strategy in the gorilla. In S. T. Parker & K. R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 333-355). New York: Cambridge University Press.

Gómez, J.-C. (1991). Visual behaviour as a window for reading the mind of others in primates. In A. Whiten (Ed.), *Natural Theories of Mind: Evolution, Development and Simulation of Everyday Mindreading* (pp. 195-207). Oxford: Basil Blackwell Ltd.

Gómez, J.-C. (1996). Ostensive behavior in apes. In A. E. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes*. Cambridge: Cambridge University Press.

Gómez, J.-C. (1999). Development of sensorimotor intelligence in infant gorillas: the manipulation of objects in problem-solving and exploration. In S. T. Parker, R. W. Mitchell & H. L. Miles (Eds.), *The Mentalities of Gorillas and Orangutans: Comparative Perspectives* (pp. 160-179). Cambridge: Cambridge University Press.

Gómez, J.-C. (2005). Species comparative studies and cognitive development. *TRENDS in Cognitive Sciences, 9*(3), 118-125.

Gómez, J.-C. (2007). Pointing behaviors in apes and human infants: a balanced interpretation. *Child Development, 78*(3), 729-734.

Gómez, J.-C. (2008). The evolution of pretence: from intentional availability to intentional non-existence. *Mind & Language, 23*(5), 586-606.

Gómez, J.-C. (2009). Embodying meaning: insights from primates, autism, and Brentano. *Neural networks : the official journal of the International Neural Network Society, 22*, 190-196.

Gómez, J.-C. (2010). The ontogeny of triadic cooperative interactions with humans in an infant gorilla. *Interaction Studies, 11*(3), 353-379.

Gómez, J. C. (2010). The emergence of eye contact as an intersubjective signal in an infant gorilla: implications for models of early social cognition. *Accion Psicologica, 7*(2), 35-43.

Goossens, B. M. A. (2008). *There is more to gaze than meets the eye: How animals perceive the visual behaviour of others.* Utrecht University.

Gyóri, B., Gácsi, M., & Miklósi, Á. (2010). Friend or foe: context dependent sensitivity to human behaviour in dogs. *Applied Animal Behaviour Science, 128*, 69-77.

Hall, E. T. (1963). A system for the notation of proxemic behavior. *American*

Anthropologist, 65(5), 1003-1026.
Hall, E. T., Birdwhistell, R. L., Bock, B., Bohannan, P., Jr., A. R. D., Durbin, M., et al. (1968). Proxemics [and comments and replies]. *Current Anthropology, 9*(2/3), 83-108.
Hampton, R. R. (1994). Sensitivity to information specifying the line of gaze of humans in sparrows (*Passer domesticus*). *Behaviour, 130*(1/2), 41-51.
Harcourt, A. H. (1979). The social relations and group structure of wild mountain gorillas. In D. A. Hamburg & E. R. McCown (Eds.), *The Great Apes* (pp. 186-192). London: The Benjamin/Cummings Publishing Company.
Hare, B., Addessi, E., Call, J., Tomasello, M., & Visalberghi, E. (2003). Do capuchin monkeys (*Cebus apella*) know what conspecifics do and do not see? *Animal Behaviour, 65*, 131-142.
Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science, 298*, 1634-1636.
Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour, 59*, 771-785.
Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour, 61*, 139-151.
Hare, B., & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology, 113*(2), 173-177.
Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *TRENDS in Cognitive Sciences, 9*(9), 439-444.
Hattori, Y., Kano, F., & Tomonaga, M. (2010). Differential sensitivity to conspecific and allospecific cues in chimpanzees and humans: a comparative eye-tracking study. *Biology Letters, 6*, 610-613.
Hebb, D. O. (1946). Emotion in man and animal; an analysis of the intuitive processes of recognition. *Psychological review, 53*, 88-106.
Heesy, C. P. (2009). Seeing in stereo: the ecology and evolution of primate binocular vision and stereopsis. *Evolutionary Anthropology, 18*, 21-35.
Held, S. D. E., & Špinka, M. (2011). Animal play and animal welfare. *Animal Behaviour, 81*, 891-899.
Henry, J. D., & Herrero, S. M. (1974). Social play in the American black bear: its similarity to canid social play and an examination of its identifying characteristics. *American Zoologist, 14*(1), 371-389.
Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews, 69*, 207-231.
Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences, 21*, 101-114; discussion 115-148.
Hirata, S., Fuwa, K., Sugama, K., Kusunoki, K., & Fujita, S. (2010). Facial perception of conspecifics: chimpanzees (*Pan troglodytes*) preferentially attend to proper orientation and open eyes. *Animal Cognition, 13*(4).
Hoff, M. P., Nadler, R. D., & Maple, T. L. (1981). The development of infant play in a captive group of lowland gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology, 1*, 65-72.
Hooff, J. A. R. A. M. V. (1973). Structural analysis of behaviour in chimpanzees. In M.

V. Cranach & I. Vine (Eds.), *Social Communication and Movement: Studies of Interaction and Expression in Man and Chimpanzee* (Vol. 75-162). New York: Academic Press.

Hopfinger, J. B., & Mangun, G. R. (2001). Tracking the influence of reflexive attention on sensory and cognitive processing. *Cognitive, Affective, & Behavioral Neuroscience, 1*(1), 56-65.

Hopkins, W. D. (1993). Posture and reaching in chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology, 107*(2), 162-168.

Hostetter, A.B., & Alibali, M.W. (2007). Raise your hand if you're spatial: relations between verbal and spatial skills and gesture production. *Gesture, 7*(1), 73-95.

Horn, L., Virányi, Z., Miklósi, Á., Huber, L., & Range, F. (2011). Domestic dogs (*Canis familiaris*) flexibly adjust their human-directed behavior to the actions of their human partners in a problem situation. *Animal Cognition*, *15*(1), 57-71.

Horowitz, A. C. (2003). Do humans ape? Or do apes human? Imitation and intention in humans (*Homo sapiens*) and other animals. *Journal of Comparative Psychology, 117*(3), 325-336.

Horowitz, A. C. (2009). *Inside of a dog: what dogs see, smell, and know*. New York, NY: Simon & Schuster, Inc.

Horowitz, A. C. (2011). Theory of mind in dogs? Examining method and concept. *Learning & Behavior*, *39*(4), 314-317.

Horowitz, A. C., & Bekoff, M. (2007). Naturalizing anthropomorphism: behavioral prompts to our humanizing of animals. *Anthrozoos, 20*(1), 23-25.

Horton, K. E., & Caldwell, C. A. (2006). Visual co-orientation and expectations about attentional orientation in pileated gibbons (*Hylobates pileatus*). *Behavioural Processes, 72*, 65-73.

Hrdy, S. B. (1977). Infanticide as a primate reproductive strategy. *American Scientist, 65*(1), 40-49.

Hrdy, S. B. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology, 1*, 13-40.

Imura, T., & Tomonaga, M. (2003). Perception of depth from shading in infant chimpanzees (*Pan troglodytes*). *Animal Cognition, 6*, 253-258.

Imura, T., & Tomonaga, M. (2009). Moving shadows contribute to the corridor illusion in a chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology, 123*(3), 280-286.

Imura, T., Yamaguchi, M. K., Kanazawa, S., Shirai, N., Otsuka, Y., Tomonaga, M., et al. (2006). Perception of motion trajectory of object from the moving cast shadow in infants. *Vision Research, 46*, 652-657.

Itakura, S. (2004). Gaze-following and joint visual attention in nonhuman animals. *Japanese Psychological Research, 46*(3), 216-226.

Iversen, I. H., & Matsuzawa, T. (2003). Development of interception of moving targets by chimpanzees (*Pan troglodytes*) in an automated task. *Animal Cognition, 6*, 169-183.

Iwaniuk, A. N., Nelson, J. E., & Pellis, S. M. (2001). Do big-brained animals play more? Comparative analyses of play and relative brain size in mammals. *Journal of*

Comparative Psychology, 115(1), 29-41.
Jaime, M., Lopez, J. P., & Lickliter, R. (2009). Bobwhite quail (*Colinus virginianus*) hatchlings track the direction of human gaze. *Animal Cognition, 12*, 559-565.
Jenkins, R. (2007). The lighter side of gaze perception. *Perception, 36*(8), 1266-1268.
Kalan, A. K., & Rainey, H. J. (2009). Hand-clapping as a communicative gesture by wild female swamp gorillas. *Primates, 50*(2).
Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: two factors controlling apes' begging behavior from humans. *Animal Cognition, 7*(4), 216-223.
Kaminski, J., Call, J., & Tomasello, M. (2008). Chimpanzees know what others know, but not what they believe. *Cognition, 109*, 224-234.
Kaminski, J., Neumann, M., Bräuer, J., Call, J., & Tomasello, M. (2011). Dogs, *Canis familiaris*, communicate with humans to request but not to inform. *Animal Behaviour*, *82*(4), 651-658.
Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour, 69*, 11-18.
Kaminski, J., Schulz, L., & Tomasello, M. (2012). How dogs know when communication is intended for them. *Developmental Science, 15*(2), 222-232.
Kano, F., & Tomonaga, M. (2009). How chimpanzees look at pictures: a comparative eye-tracking study. *Proceedings of the Royal Society of London B, 276*, 1949-1955.
Kano, F., & Tomonaga, M. (2010a). Attention to emotional scenes including whole-body expressions in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 124*(3), 287-294.
Kano, F., & Tomonaga, M. (2010). Face scanning in chimpanzees and humans: continuity and discontinuity. *Animal Behaviour, 79*, 227-235.
Kano, F., & Tomonaga, M. (2011). Perceptual mechanism underlying gaze guidance in chimpanzees and humans. *Animal cognition, 14*, 377-386.
Kaplan, G., & Rogers, L. J. (2002). Patterns of gazing in orangutans (*Pongo pygmaeus*). *International Journal of Primatology, 23*(3), 501-526.
Kawakami, K., Takai-Kawakami, K., Tomonaga, M., Suzuki, J., Kusaka, T., & Okai, T. (2006). Origins of smile and laughter: A preliminary study. *Early Human Development, 82*, 61-66.
Kehmeier, S., Schloegl, C., Scheiber, I. B. R., & Weib, B. M. (2011). Early development of gaze-following into distant space in juvenile Greylag geese (*Anser anser*). *Animal Cognition, 14*, 477-485.
Kemp, R., McManus, C., & Pigott, T. (1990). Sensitivity to the displacement of facial features in negative and inverted images. *Perception, 19*, 531-543.
King, B. J., & Shanker, S. G. (2003). How can we know the dancer from the dance? The dynamic nature of African great ape social communication. *Anthropological Theory, 3*(1), 5-26.
Kis, A., Topál, J., Gácsi, M., Range, F., Huber, L., Miklósi, A., et al. (2012). Does the A-not-B error in adult pet dogs indicate sensitivity to human communication? *Animal Cognition*.
Knapp, M. L., & Hall, J. A. (2010). *Nonverbal communication in human interaction* (7th

ed.). Boston, MA: Wadsworth Cengage Learning.
Knapp, S., McCulley, J. P., Alvarado, T. P., & Hogan, R. N. (2007). Comparative ocular anatomy of the western lowland gorilla. *Veterinary Ophthalmology, 10*(6), 357-362.
Knobloch, H., & Pasamanick, B. (1959). Gross motor behavior in an infant gorilla. *Journal of Comparative and Physiological Psychology, 52*(5), 559-563.
Kobayashi, H., & Hashiya, K. (2011). The gaze that grooms: contribution of social factors to the evolution of primate eye morphology. *Evolution and Human Behavior, 32*, 157-165.
Kobayashi, H., & Kohshima, S. (2001). Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye. *Journal of Human Evolution, 40*, 419-435.
Kutsukake, N. (2006). The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology, 112*, 581-591.
Kutsukake, N. (2007). Conspecific influences on vigilance behavior in wild chimpanzees. *International Journal of Primatology, 28*, 907-918.
Kuwahata, H., Adachi, I., Fujita, K., Tomonaga, M., & Matsuzawa, T. (2004). Development of schematic face preference in macaque monkeys. *Behavioural processes, 66*(1), 17-21.
Kuze, N., Malim, T. P., & Kohshima, S. (2005). Developmental changes in the facial morphology of the Borneo orangutan (*Pongo pygmaeus*): possible signals in visual communication. *American Journal of Primatology, 65*, 353-376.
Lakatos, G., Soproni, K., Dóka, A., & Miklósi, A. (2009). A comparative approach to dogs' (*Canis familiaris*) and human infants' comprehension of various forms of pointing gestures. *Animal cognition, 12*, 621-631.
Langton, S. R. H. (2000). The mutual influence of gaze and head orientation in the analysis of social attention direction. *The Quarterly Journal of Experimental Psychology, 53A*(3), 825-845.
Langton, S. R. H., Watt, R. J., & Bruce, V. (2000). Do the eyes have it? Cues to the direction of social attention. *Trends in Cognitive Sciences, 4*(2), 50-58.
Laube, I., Kamphuis, S., Dicke, P. W., & Thier, P. (2011). Cortical processing of head- and eye-gaze cues guiding joint social attention. *NeuroImage, 54*, 1643-1653.
Lazar, J. W., & Beckhorn, G. D. (1974). Social play or the development of social behavior in ferrets (*Mustela putorius*)? *American Zoologist, 14*(1), 405-414.
Leavens, D. A. (2006). It takes time and experience to learn how to interpret gaze in mentalistic terms. *Child Development, 15*, 187-190.
Leavens, D. A., & Hopkins, W. D. (1999). The whole-hand point: the structure and function of pointing from a comparative perspective. *Journal of Comparative Psychology, 113*(4), 417-425.
Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the point of chimpanzee pointing: epigenesis and ecological validity. *Current Directions in Psychological Science, 14*(4), 185-189.
Leavens, D. A., Hopkins, W. D., & Thomas, R. K. (2004). Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 118*(1), 48-57.
Leavens, D. A., & Racine, T. P. (2009). Joint attention in apes and humans. *Journal of*

Consciousness Studies, 16(6-8), 240-267.
Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development, 76*(1), 291-306.
Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2010). Multimodal communication by captive chimpanzees (*Pan troglodytes*). *Animal Cognition, 13*, 33-40.
Lee, B. B. (2010). Visual pathways and psychophysical channels in the primate. *The Journal of Physiology, 589*(1), 41-47.
Leeuwen, E. v., Zimmermann, E., & Ross, M. D. (2010). Responding to inequities: gorillas try to maintain their competitive advantage during play fights. *Biology Letters*.
Lewis, K. P., & Barton, R. A. (2004). Playing for keeps: evolutionary relationships between social play and the cerebellum in nonhuman primates. *Human Nature, 15*(1), 5-21.
Lewis, K. P., & Barton, R. A. (2006). Amygdala size and hypothalamus size predict social play frequency in nonhuman primates: a comparative analysis using independent contrasts. *Journal of Comparative Psychology, 120*(1), 31-37.
Li, Y., Guo, S., Ji, W., He, G., Wang, X., & Li, B. (2011). Social play behavior in infant Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling mountains, China. *American Journal of Primatology, 73*, 845-851.
Liang, D., Alvarado, T. P., Oral, D., Vargas, J. M., Denena, M. M., & McCulley, J. P. (2005). Ophthalmic examination of the captive western lowland gorilla (*Gorilla gorilla gorilla*). *Journal of Zoo and Wildlife Medicine, 36*(3), 430-433.
Liebal, K., Call, J., & Tomasello, M. (2004). Use of gesture sequences in chimpanzees. *American Journal of Primatology, 64*, 377-396.
Liebal, K., Pika, S., Call, J., & Tomasello, M. (2004). To move or not to move: How apes adjust to the attentional states of others. *Interaction Studies, 5*(2), 199-219.
Liebal, K., Pika, S., & Tomasello, M. (2006). Gestural communication of orangutans. *Gesture, 6*(1), 1-38.
Littlejohn, S. W., & Foss, K. A. (2008). *Theories of human communication* (9th ed.). Belmont, CA: Thomson Wadsworth Higher Education.
Loretto, M.-C., Schloegl, C., & Bugnyar, T. (2010). Northern bald ibises follow others' gaze into distant space but not behind barriers. *Biology Letters, 6*, 14-17.
Lyn, H. (2010). Environment, methodology, and the object-choice task in apes: evidence for declarative comprehension and implications for the evolution of language. *Journal of Evolutionary Psychology, 8*(4), 333-349.
MacLean, E. L., & Hare, B. (2011). Bonobos and chimpanzees infer the target of another's attention. *Animal Behaviour*, *83*(2), 345-353.
Macrae, C. N., Hood, B. M., Milne, A. B., Rowe, A. C., & Mason, M. F. (2002). Are you looking at me? Eye gaze and person perception. *Psychological Science, 13*(5), 460-464.
Maestripieri, D., Ross, S. K., & Megna, N. L. (2002). Mother-infant interactions in western lowland gorillas (*Gorilla gorilla gorilla*): spatial relationships, communication, and opportunities for social learning. *Journal of Comparative Psychology, 116*(3), 219-227.
Maestripieri, D., & Ross, S. R. (2004). Sex differences in play among western lowland

gorilla (*Gorilla gorilla gorilla*) infants: implications for adult behavior and social structure. *American Journal of Physical Anthropology, 123*(1), 52-61.
Maple, T., & Zucker, E. L. (1978). Ethological studies of play behavior in captive great apes. In E. O. Smith (Ed.), *Social Play In Primates* (pp. 113-142). New York: Academic Press, Inc.
Margulis, S. W., Steele, G. R., & Kleinfelder, R. E. (2012). Use of buckets as tools by western lowland gorillas. *Zoo Biology, 7*, 1-7.
Maros, K., Gácsi, M., & Miklósi, A. (2008). Comprehension of human pointing gestures in horses (*Equus caballus*). *Animal cognition, 11*, 457-466.
Marsh, H. L., & MacDonald, S. E. (2008). The use of perceptual features in categorization by orangutans (*Pongo abelli*). *Animal Cognition, 11*, 569-585.
Marticorena, D. C. W., Ruiz, A. M., Mukerji, C., Goddu, A., & Santos, L. R. (2011). Monkeys represent others' knowledge but not their beliefs. *Developmental Science, 14*(6), 1406-1416.
Martin, P., & Caro, T. M. (1985). On the functions of play and its role in behavioral development. *Advances in the Study of Behavior, 15*, 59-103.
Martin, R. D. (1990). Primate origins and evolution: a phylogenetic reconstruction. Princeton: Princeton University Press.
Mason, G. J. (1991). Stereotypies: a critical review. *Animal Behaviour, 41*(6), 1015-1037.
Matsuno, T., & Fujita, K. (2009). A comparative psychophysical approach to visual perception in primates. *Primates*, *50*(2), 121-130.
McGrew, W. C., L. F. Marchant, et al., Eds. (1996). Great Ape Societies. Cambridge, Cambridge University Press.
Meguerditchian, A., Gardner, M. J., Schapiro, S. J., & Hopkins, W. D. (2012). The sound of one-hand clapping: handedness and perisylvian neural correlates of a communicative gesture in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 279*(1735), 1959-1966.
Meltzoff, A. N., & Moore, M. K. (1977). Imitation of facial and manual gestures by human neonates. *Science, 198*(4312), 75-78.
Menzel, E. W. (1973). Leadership and communication in young chimpanzees. In W. Montagna (Ed.), *Symposia of the Fourth International Congress of Primatology: Precultural primate behavior* (Vol. 1, pp. 192-225). Basel, Switzerland: Coop-Schweiz.
Micheletta, J., & Waller, B. M. (2011). Friendship affects gaze-following in a tolerant species of macaque, *Macaca nigra*. *Animal Behaviour*, *83*(2), 459-467.
Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Current Biology, 13*, 763-766.
Miklósi, Á., Polgárdi, R., Topál, J., & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition, 1*, 113-121.
Miklósi, Á., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition, 9*, 81-93.
Miklósi, Á., Topál, J., & Csányi, V. (2004). Comparative social cognition: what can dogs teach us. *Animal Behaviour, 67*, 995-1004.
Millikan, R. G. (2000). *Naturalizing Intentionality.* Paper presented at the Philosophy of Mind, Proceedings of the 20th World Congress of Philosophy.

Mitchell, R. W., & Thompson, N. S. (1986). Deception in play between dogs and people. In R. W. Mitchell & N. S. Thompson (Eds.), *Deception: perspectives on human and nonhuman deceit* (pp. 193-204). Albany, New York: State University of New York Press.

Mulcahy, N. J., & Hedge, V. (2012). Are great apes tested with an abject object-choice task? *Animal Behaviour*, *83*(2), 313-321.

Müller-Schwarze, D. (1984). Analysis of play behaviour: what do we measure and when? In P. K. Smith (Ed.), *Play In Animals and Humans* (pp. 147-158). Oxford: Basil Blackwell, Inc.

Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2003). Preference for human direct gaze in infant chimpanzees (*Pan troglodytes*). *Cognition, 89*(2), 113-124.

Nakata, R., & Osada, Y. (2012). The Thatcher illusion in squirrel monkeys (*Saimiri sciureus)*. *Animal Cognition*.

Nakato, E., Otsuka, Y., Konuma, H., Kanazawa, S., Yamaguchi, M. K., & Tomonaga, M. (2009). Perception of illusory shift of gaze direction by infants. *Infant Behavior & Development, 32*(4), 422-428.

Nishida, T., & Inaba, A. (2009). Pirouettes: the rotational play of wild chimpanzees. *Primates*, *50*(4), 333-341.

Norscia, I., & Palagi, E. (2011). When play is a family business: adult play, hierarchy, and possible stress reduction in common marmosets. *Primates, 52*(2), 101-104.

Öhman, A. (2002). Automaticity and the amygdala: nonconscious responses to emotional faces. *Current Directions in Psychological Science, 11*(2), 62-66.

Okamoto, S., Tomonaga, M., Ishii, K., Kawai, N., Tanaka, M., & Matsuzawa, T. (2002). An infant chimpanzee (*Pan troglodytes*) follows human gaze. *Animal Cognition, 5*, 107-114.

Ogden, J., Baker, A., Beck, B. B., Bennett, C. duBois, T., Cox, C., Gold, K., Fernandes, D., Glick, C., Porton, I., & Mellen, J. (1991). Collection of gorilla ethograms.

Okamoto-Barth, S., Call, J., & Tomasello, M. (2007). Great apes' understanding of other individuals' lines of sight. *Psychological Science, 18*(5), 462-468.

Olk, B., Symons, L. A., & Kingston, A. (2008). Take a look at the bright side: effects of contrast polarity on gaze direction judgments. *Perception & Psychophysics, 70*(7), 1298-1304.

Ondobaka, S., Lange, F. P. D., Newman-Norlund, R. D., Wiemers, M., & Bekkering, H. (2012). Interplay between action and movement intentions during social interaction. *Psychological Science*.

Orban, G. A. (2008). Higher order visual processing in macaque extrastriate cortex. *Physiology Review, 88*, 59-89.

Orban, G. A., Essen, D. V., & Vanduffel, W. (2004). Comparative mapping of higher visual areas in monkeys and humans. *Trends in Cognitive Sciences, 8*(7), 315-324.

Ortega, J. C., & Bekoff, M. (1987). Avian play: comparative evolutionary and developmental trends. *The Auk, 104*(2), 338-341.

Ortolani, A. (1999). Spots, stripes, tail tips and dark eyes: predicting the function of carnivore colour patterns using the comparative method. *Biological Journal of the Linnean Society, 67*, 433-476.

Pack, A. A., & Herman, L. M. (2006). Dolphin social cognition and joint attention: our current understanding. *Aquatic Mammals, 32*, 443-460.

Pal, S. K. (2010). Play behaviour during early ontogeny in free-ranging dogs (*Canis familiaris*). *Applied Animal Behaviour Science, 126*, 140-153.

Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): implications for natural social systems and interindividual relationships. *American Journal of Physical Anthropology, 129*, 418-426.

Palagi, E. (2009). Adult play fighting and potential role of tail signals in ringtailed lemurs (*Lemur catta*). *Journal of Comparative Psychology, 123*(1), 1-9.

Palagi, E., Antonacci, D., & Cordoni, G. (2007). Fine-tuning of social play in juvenile lowland gorillas (*Gorilla gorilla gorilla*). *Developmental Psychobiology*, 433-445.

Palagi, E., & Cordoni, G. (2009). Postconflict third-party affiliation in canis lupus: do wolves share similarities with the great apes? *Animal Behaviour, 78*, 979-986.

Palagi, E., Cordoni, G., & Borgognini Tarli, S. M. (2004). Immediate and delayed benefits of play behaviour: new evidence from chimpanzees (*Pan troglodytes*). *Ethology, 110*, 949-962.

Palagi, E., & Mancini, G. (2011). Playing with the face: playful facial "chattering" and signal modulation in a monkey species (*Theropithecus gelada*). *Journal of Comparative Psychology, 125*(1), 11-21.

Palagi, E., Paoli, T., & Tarli, S. B. (2006). Short-term benefits of play behavior and conflict prevention in *Pan paniscus*. *International Journal of Primatology, 27*(5), 1257-1270.

Panksepp, J. (2005). Affective consciousness: core emotional feelings in animals and humans. *Consciousness and Cognition, 14*(1), 30-80.

Parker, S. T. (1999). The development of social roles in the play of an infant gorilla and its relationship to sensorimotor intellectual development. In S. T. Parker, R. W. Mitchell & H. L. Miles (Eds.), *The mentalities of gorillas and orangutans: comparative perspectives* (pp. 367-393). New York: Cambridge University Press.

Parkinson, B. (2005). Do facial movements express emotions or communicate motives? *Personality and Social Psychology Review, 9*, 278.

Parnell, R. J., & Buchanan-Smith, H. M. (2001). An unusual social display by gorillas. *Nature, 412*, 294.

Parr, L. A., Cohen, M., & de Waal, F. (2005). Influence of social context on the use of blended and graded facial displays in chimpanzees. *International Journal of Primatology, 26*(1), 73-103.

Parr, L. A., Hecht, E., Barks, S. K., Preuss, T. M., & Votaw, J. R. (2008). Face processing in the chimpanzee brain. *Current Biology, 19*, 1-4.

Parr, L. A., Heintz, M., & Akamagwuna, U. (2006). Three studies on configural face processing by chimpanzees. *Brain and Cognition, 62*, 30-42.

Parr, L. A., & Maestripieri, D. (2003). Nonvocal communication. In D. Maestripieri (Ed.), *Primate Psychology* (pp. 324-358). Cambridge: Harvard University Press.

Parr, L. A., & Taubert, J. (2011). The importance of surface-based cues for face discrimination in non-human primates. *Proceedings of the Royal Society B: Biological Sciences, 278*, 1964-1972.

Parr, L. A., Waller, B. M., & Fugate, J. (2005). Emotional communication in primates:

implications for neurobiology. *Current Opinion in Neurobiology, 15*, 716-720.
Peignot, P., & Anderson, J. R. (1999). Use of experimenter-given manual and facial cues by gorillas (*Gorilla gorilla*) in an object-choice task. *Journal of Comparative Psychology, 113*(3), 253-260.
Pellis, S. M. (1997). Targets and tactics: the analysis of moment-to-moment decision making in animal combat. *Aggressive Behavior, 23*, 107-129.
Pellis, S. M. (2002). Keeping in touch: play fighting and social knowledge. In M. Bekoff, C. Allen & G. M. Burghardt (Eds.), *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition* (pp. 421-427). Cambridge, Massachusetts: The MIT Press.
Pellis, S. M., & Iwaniuk, A. N. (1999). The problem of adult play fighting: a comparative analysis of play and courtship in primates. *Ethology, 105*, 783-806.
Pellis, S. M., & Iwaniuk, A. N. (2000a). Adult-adult play in primates: comparative analyses of its origin, distribution and evolution. *Ethology, 106*, 1083-1104.
Pellis, S. M., & Iwaniuk, A. N. (2000b). Comparative analyses of the role of postnatal development on the expression of play fighting. *Developmental Psychobiology, 36*(2), 136-147.
Pellis, S. M., & Pellis, V. C. (1996). On knowing it's only play: The role of play signals in play fighting. *Aggression and Violent Behavior, 1*(3), 249-268.
Pellis, S. M., & Pellis, V. C. (1997). Targets, tactics, and the open mouth face during play fighting in three species of primates. *Aggressive Behavior, 23*, 41-57.
Pellis, S. M., & Pellis, V. C. (2007). Rough-and-tumble play and the development of the social brain. *Current Directions in Psychological Science, 16*(2), 95-98.
Pellis, S. M., & Pellis, V. C. (2009). *The playful brain*: *venturing to the limits of neuroscience*. Oxford: Oneworld Publications.
Pellis, S. M., & Pellis, V. C. (2011). To whom the play signal is directed: a study of headshaking in black-handed spider monkeys (*Ateles geoffroyi*). *Journal of Comparative Psychology, 125*(1), 1-10.
Pellis, S. M., Pellis, V. C., Reinhart, C. J., & Thierry, B. (2011). The use of the bared-teeth display during play fighting in Tonkean macaques (*Macaca tonkeana*): sometimes it is all about oneself. *Journal of Comparative Psychology, 125*(4), 395-403.
Péron, F., Chardard, C., Nagle, L., & Bovet, D. (2011). Do African grey parrots (*Psittacus erithacus*) know what a human experimenter does and does not see? *Behavioural processes, 87*, 237-240.
Perrett, D. I., & Emery, N. J. (1994). Understanding the intentions of others from visual signals: neurophysiological evidence. *Cahiers de Psychologie Cognitive, 13*(5), 683-694.
Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical transactions of the Royal Society B*: *Biological sciences, 335*, 23-30.
Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., et al. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London B: Biological Sciences, 223*, 293-317.
Petrů, M., Spinka, M., Charvátová, V., & Lhota, S. (2009). Revisiting play elements and

self-handicapping in play: a comparative ethogram of five Old World monkey species. *Journal of Comparative Psychology, 123*(2), 250-263.

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning, and use. *American Journal of Primatology, 60*, 95-111.

Pika, S., Liebal, K., & Tomasello, M. (2005). Gestural communication in subadult bonobos (*Pan paniscus*): repertoire and use. *American Journal of Primatology, 65*, 39-61.

Pika, S., & Zuberbühler, K. (2008). Social games between bonobos and humans: evidence for shared intentionality? *American Journal of Primatology, 70*, 207-210.

Pitman, C. A., & Shumaker, R. W. (2009). Does early care affect joint attention in great apes (*Pan troglodytes, Pan paniscus, Pongo abelii, Pongo pygmaeus, Gorilla gorilla*)? *Journal of Comparative Psychology, 123*(3), 334-341.

Platt, M. L., & Ghazanfar, A. A. (Eds.). (2010). *Primate neuroethology*. New York: Oxford University Press, Inc.

Poirier, F. E., & Smith, E. O. (1974). Socializing functions of primate play. *American Zoologist, 14*(1), 275-287.

Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology, 3*(1), 3-25.

Poss, S. R., Kuhar, C., Stoinski, T. S., & Hopkins, W. D. (2006). Differential use of attentional and visual communicative signaling by orangutans (*Pongo pygmaeus*) and gorillas (*Gorilla gorilla*) in response to the attentional state of a human. *American Journal of Primatology, 68*, 978-992.

Povinelli, D. J., & Bering, J. M. (2002). The mentality of apes revisited. *Current Directions in Psychological Science, 11*, 115-119.

Povinelli, D. J., & Eddy, T. J. (1996). Chimpanzees: joint visual attention. *Psychological Science, 7*(3), 129-135.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences, 4*, 515-526.

Preuschoft, S. (2000). Primate faces and facial expressions. *Social Research, 67*(1), 245-272.

Proops, L., & McComb, K. (2010). Attributing attention: the use of human-given cues by domestic horses (*Equus caballus*). *Animal Cognition, 13*, 197-205.

Provine, R. R., Cabrera, M. O., Brocato, N. W., & Krosnowski, K. A. (2011). When the whites of the eyes are red: a uniquely human cue. *Ethology, 117*, 395-399.

Range, F., & Virányi, Z. (2011). Development of gaze-following abilities in wolves (*Canis lupus*). *PLoS ONE, 6*(2), e16888.

Re, D. E., Whitehead, R. D., Xiao, D., & Perrett, D. I. (2011). Oxygenated-blood colour change thresholds for perceived facial redness, health, and attractiveness. *PLoS ONE, 6*(3), 1-5.

Rensch, B. (1978). Play and art in apes in monkeys. In W. Montagna (Ed.), *Symposia of the Fourth International Congress of Primatology: Precultural Primate Behavior* (pp. 102-123). Basel, Switzerland: Coop-Schweiz.

Ricciardelli, P., Baylis, G., & Driver, J. (2000). The positive and negative of human expertise in gaze perception. *Cognition, 77*, B1-B14.

Ricciardelli, P., Betta, E., Pruner, S., & Turatto, M. (2009). Is there a direct link between gaze perception and joint attention behaviours? Effects of gaze contrast polarity on oculomotor behaviour. *Experimental Brain Research, 194*, 347-357.

Rigato, S., Menon, E., Johnson, M. H., Faraguna, D., & Farroni, T. (2011). Direct gaze may modulate face recognition in newborns. *Infant and Child Development, 20*, 20-34.

Rooijakkers, E. F., Kaminski, J., & Call, J. (2009). Comparing dogs and great apes in their ability to visually track object transpositions. *Animal Cognition*, *12*(6), 789-796.

Rooney, N. J., Bradshaw, J. W. S., & Robinson, I. H. (2001). Do dogs respond to play signals given by humans. *Animal Behaviour, 61*, 715-722.

Rosati, A. G., & Hare, B. (2009). Looking past the model species: diversity in gaze-following skills across primates. *Current Opinion in Neurobiology, 19*, 45-51.

Ross, C. F., & Kirk, E. C. (2007). Evolution of eye size and shape in primates. *Journal of Human Evolution, 52*, 294-313.

Ross, M. D., Menzler, S., & Zimmermann, E. (2008). Rapid facial mimicry in orangutan play. *Biology Letters, 4*, 27-30.

Ross, M. D., Owren, M. J., & Zimmermann, E. (2010). The evolution of laughter in great apes and humans. *Communicative & Integrative Biology, 3*(2), 191-194.

Ruiz, A., Gómez, J. C., Roeder, J. J., & Byrne, R. W. (2009). Gaze-following and gaze priming in lemurs. *Animal cognition, 12*, 427-434.

Sadr, J., Jarudi, I., & Sinha, P. (2003). The role of eyebrows in face recognition. *Perception, 32*, 285-293.

Sartori, L., Becchio, C., & Castiello, U. (2011). Cues to intention: the role of movement information. *Cognition*.

Scerif, G., Gómez, J.-C., & Byrne, R. W. (2004). What do Diana monkeys know about the focus of attention of a conspecific? *Animal Behaviour, 68*, 1239-1247.

Schaller, G. (1963). *The mountain gorilla: ecology and behavior*. Chicago: The University of Chicago Press.

Schaller, G. (1995). Gentle Gorillas, Turbulent Times. *National Geographic, 188,* 66.

Schloegl, C., Kotrschal, K., & Bugnyar, T. (2007). Gaze-following in common ravens, *Corvus corax*: ontogeny and habituation. *Animal Behaviour, 74*, 769-778.

Schloegl, C., Kotrschal, K., & Bugnyar, T. (2008). Do common ravens (*Corvus corax*) rely on human or conspecific cues to detect hidden food? *Animal Cognition, 11*, 231-241.

Schmidt, J., Scheid, C., Kotrschal, K., Bugnyar, T., & Schloegl, C. (2011). Gaze direction - a cue for hidden food in rooks (*Corvus frugilegus*)? *Behavioural Processes*, *88*(2), 88-93.

Schmittbuhl, M., Minor, J.-M. L., Allenbach, B., & Schaaf, A. (1999). Shape of the orbital opening: individual characterization and analysis of variability in modern humans, *Gorilla gorilla,* and *Pan troglodytes*. *Annals of Anatomy, 181*, 299-307.

Schneider, C., Call, J., & Liebal, K. (2012). Onset and early use of gestural communication in nonhuman great apes. *American Journal of Primatology, 113*, 102-113.

Scott, E., & Panksepp, J. (2003). Rough-and-tumble play in human children. *Aggressive Behavior, 29*, 539-551.

Seyama, J., & Nagayama, R. (2005). The effect of torso direction on the judgment of eye direction. *Visual Cognition, 12*(1), 103-116.

Shapiro, A. D., Janik, V. M., & Slater, P. J. B. (2003). A gray seal's (*Halichoerus grypus*) responses to experimenter-given pointing and directional cues. *Journal of Comparative Psychology, 117*(4), 355-362.

Shepherd, S. V. (2010). Following gaze: gaze-following behavior as a window into social cognition. *Frontiers in Integrative Neuroscience, 4*, 1-13.

Shepherd, S. V., & Platt, M. L. (2008). Spontaneous social orienting and gaze-following in ringtailed lemurs (*Lemur catta*). *Animal Cognition, 11*, 13-20.

Shillito, D. J., Gordon G. Gallup, J., & Beck, B. B. (1999). Factors affecting mirror behaviour in western lowland gorillas, *Gorilla gorilla*. *Animal Behaviour, 57*, 999-1004.

Shillito, D. J., Shumaker, R. W., Jr., G. G. G., & Beck, B. B. (2005). Understanding visual barriers: evidence for Level 1 perspective taking in an orang-utan, *Pongo pygmaeus*. *Animal Behaviour, 69*, 679-687.

Sinha, P. (2000). Here's looking at you, kid. *Perception, 29*, 1005-1008.

Siviy, S. M., Baliko, C. N., & Bowers, K. S. (1997). Rough-and-tumble play behavior in Fischer-344 and Buffalo rats: effects of social isolation. *Physiology and Behavior, 61*(4), 597-602.

Siviy, S. M., Harrison, K. A., & McGregor, I. S. (2006). Fear, risk assessment and playfulness in the juvenile rat. *Behavioral neuroscience, 120*, 49.

Siviy, S. M., Love, N. J., DeCicco, B. M., Giordano, S. B., & Seifert, T. L. (2003). The relative playfulness of juvenile Lewis and Fischer-344 rats. *Physiology and Behavior, 80*, 385-394.

Smith, E. O. (1978). A historical view on the study of play: statement of the problem. In E. O. Smith (Ed.), *Social Play In Primates* (pp. 1-32). New York: Academic Press, Inc.

Smith, P. K. (1982). Does play matter? Functional and evolutionary aspects of animal and human play. *Behavioral and Brain Sciences, 5*, 139-184.

Soproni, K., Miklósi, Á., Topál, J., & Csányi, V. (2002). Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology, 116*(1), 27-34.

Sousa, A. A., Sherwood, C. C., Schleicher, A., Amunts, K., MacLeod, C. E., Hof, P. R., et al. (2010). Comparative cytoarchitectural analyses of striate and extrastriate areas in Hominoids. *Cerebral Cortex, 20*, 966-981.

Starmans, C., & Bloom, P. (2012). Windows to the soul: children and adults see the eyes as the location of the self. *Cognition, 123*, 313-318.

Stephen, I. D., Coetzee, V., & Perrett, D. I. (2011). Carotenoid and melanin pigment coloration affect perceived human health. *Evolution and Human Behavior, 32*, 216-227.

Stojan-Dolar, M., & Heymann, E. W. (2010). Vigilance in a cooperatively breeding primate. *International Journal of Primatology, 31*, 95-116.

Sugita, Y. (2008). Face perception in monkeys reared with no exposure to faces. *PNAS, 105*(1), 394-398.

Suter, H. C., & Huntingford, F. A. (2002). Eye colour in juvenile Atlantic salmon: effects of social status, aggression and foraging success. *Journal of Fish Biology, 61*,

606-614.
Suzuki, M., Izawa, A., Takahashi, K., & Yamazaki, T. (2008). The coordination of eye, head, and arm movements during rapid gaze orienting and arm pointing. *Experimental Brain Research, 184*, 579-585.
Symons, D. (1974). Aggressive play and communication in Rhesus monkeys (*Macaca mulatta*). *American Zoologist, 14*, 317-322.
Takeshita, H., Fragaszy, D., Mizuno, T., Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2005). Exploring by doing: how young chimpanzees discover surfaces through actions with objects. *Infant Behavior & Development, 28*, 316-328.
Tanner, J. E. (2004). Gestural phrases and gestural exchanges by a pair of zoo-living lowland gorillas. *Gesture, 4*(1), 1-24.
Tanner, J. E., & Byrne, R. W. (1993). Concealing facial evidence of mood: perspective-taking in a captive gorilla? *Primates, 34*(4), 451-457.
Tanner, J. E., & Byrne, R. W. (1996). Representation of action through iconic gesture in a captive lowland gorilla. *Current Anthropology, 37*(1), 163-173.
Tanner, J. E., & Byrne, R. W. (1999). The development of spontaneous gestural communication in a group of zoo-living lowland gorillas. In S. T. Parker, R. W. Mitchell & H. L. Miles (Eds.), *The Mentalities of Gorillas and Orangutans: Comparative Perspectives* (pp. 211-240). Cambridge: Cambridge University Press.
Tanner, J. E., & Byrne, R. W. (2010). Triadic and collaborative play by gorillas in social games with objects. *Animal Cognition*, *13*(4), 591-607.
Taubert, J., & Parr, L. A. (2009). Visual expertise does not predict the composite effect across species: A comparison between spider (*Ateles geoffroyi*) and rhesus (*Macaca mulatta*) monkeys. *Brain and Cognition, 71*, 187-195.
Tempelmann, S., Kaminski, J., & Liebal, K. (2011). Focus on the essential: all great apes know when others are being attentive. *Animal Cognition*, *14*(3), 433-439.
Tipples, J. (2002). Eye gaze is not unique: automatic orienting in response to uninformative arrows. *Psychonomic Bulletin & Review, 9*(2), 314-318.
Tipples, J. (2005). Orienting to eye gaze and face processing. *Journal of Experimental Psychology, 31*(5), 843-856.
Tirassa, M., Bosco, F. M., & Colle, L. (2006). Rethinking the ontogeny of mindreading. *Consciousness and Cognition, 15*, 197-217.
Todorović, D. (2006). Geometrical basis of perception of gaze direction. *Vision research, 46*, 3549-3562.
Todorović, D. (2009). The effect of face eccentricity on the perception of gaze direction. *Perception, 38*, 109-132.
Tomasello, M. (2008). *Origins of human communication*. Cambridge: MIT Press.
Tomasello, M., & Call, J. (2007). Intentional communication in nonhuman primates. In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys* (pp. 1-15). Mahwah: Lawrence Erlbaum Associates.
Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour, 55*, 1063-1069.
Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees understand psychological states - the question is which ones and to what extent. *Trends in Cognitive Sciences, 7*(4), 153-156.

Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: a trans-generational study. *Primates, 35*(2), 137-154.

Tomasello, M., Gust, D., & Frost, G. T. (1989). A longitudinal investigation of gestural communication in young chimpanzees. *Primates, 30*(1), 35-50.

Tomasello, M., Hare, B., & Agnetta, B. (1999). Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Animal Behaviour, 58*, 769-777.

Tomasello, M., Hare, B., & Fogleman, T. (2001). The ontogeny of gaze-following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Animal Behaviour, 61*, 335-343.

Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze-following of great apes and human infants: the cooperative eye hypothesis. *Journal of Human Evolution, 52*, 314-320.

Tomasello, M., & Rakoczy, H. (2003). What makes human cognition unique? From individuals to shared to collective intentionality. *Mind & Language, 18*(2), 121-147.

Tomonaga, M. (2007). Is chimpanzee (*Pan troglodytes*) spatial attention reflexively triggered by the gaze cue? *Journal of Comparative Psychology, 121*(2), 156-170.

Tomonaga, M., & Imura, T. (2009). Human gestures trigger different attentional shifts in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). *Animal Cognition*, *12*, 11-18.

Tomonaga, M., & Imura, T. (2010). Visual search for human gaze direction by a chimpanzee (*Pan troglodytes*). *PLoS ONE, 5*(2), 1-11.

Tóth, L., Gácsi, M., Topál, J., & Miklósi, Á. (2008). Playing styles and possible causative factors in dogs' behaviour when playing with humans. *Applied Animal Behaviour Science, 114*(3-4), 473-484.

Treue, S. (2001). Neural correlates of attention in primate visual cortex. *Trends in Cognitive Sciences, 24*(5), 295-300.

Treves, A. (1997). Primate natal coats: a preliminary analysis of distribution and function. *American Journal of Physical Anthropology, 104*, 47-70.

Tschudin, A., Call, J., Dunbar, R. I. M., Harris, G., & van der Elst, C. (2001). Comprehension of signs by dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology, 115*(1), 100-105.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2011). Can your dog read your mind? Understanding the causes of canine perspective taking. *Learning & Behavior*, *39*(4), 289-302.

Ushitani, T., Imura, T., & Tomonaga, M. (2010). Object-based attention in chimpanzees (*Pan troglodytes*). *Vision Research, 50*, 577-584.

Veilleux, C. C., & Lewis, R. J. (2011). Effects of habitat light intensity on mammalian eye shape. *The Anatomical Record Part A, 294*, 905-914.

Vick, S.-J., & Anderson, J. R. (2003). Use of human visual attention cues by olive baboons (*Papio anubis*) in a competitive task. *Journal of Comparative Psychology, 117*(2), 209-216.

Vick, S.-J., Bovet, D., & Anderson, J. R. (2001). Gaze discrimination learning in olive baboons (*Papio anubis*). *Animal Cognition, 4*, 1-10.

Vick, S.-J., Waller, B. M., Parr, L. A., Pasqualini, M. C. S., & Bard, K. A. (2007). A

cross-species comparison of facial morphology and movement in humans and chimpanzees using the facial action coding system (FACS). *Journal of Nonverbal Behavior, 31*, 1-20.

Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., et al. (2008). Comprehension of human pointing gestures in young human-reared wolves (Canis lupus) and dogs (Canis familiaris). *Animal cognition, 11*, 373-387.

Vlamings, P. H. J. M., Hare, B., & Call, J. (2010). Reaching around barriers: the performance of the great apes and 3-5-year-old children. *Animal cognition, 13*, 273-285.

Vogel, A., Dlugos, C., Nuffer, R., & Birngruber, R. (1991). Optical properties of human sclera, and their consequences for transscleral laser applications. *Lasers in Surgery and Medicine, 11*, 331-340.

Voland, E. (1977). Social play behavior of the common marmoset (*Callithrix jacchus*) in captivity. *Primates, 18*, 883-901.

Vorobyev, M. (2004). Ecology and evolution of primate colour vision. *Clinical & Experimental Optometry, 87*(4/5), 230-238.

Waller, B. M., & Cherry, L. (2012). Facilitating play through communication: significance of teeth exposure in the gorilla play face. *American Journal of Primatology, 74*, 157-164.

Waller, B. M., & Dunbar, R. I. M. (2005). Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (*Pan troglodytes*). *Ethology, 111*, 129-142.

Warneken, F., Chen, F., & Tomasello, M. (2006). Cooperative activities in young children and chimpanzees. *Child Development, 77*(3), 640-663.

Watson, O. M., & Graves, T. D. (1966). Quantitative research in proxemic behavior. *American Anthropologist, 68*(4), 971-985.

Watt, R., Craven, B., & Quinn, S. (2007). A role for eyebrows in regulating the visibility of eye gaze direction. *The Quarterly Journal of Experimental Psychology, 60*(9), 1169-1177.

Watts, D. P. (1996). Comparative socio-ecology of gorillas. In W. C. McGrew, L. F. Marchant & T. Nishida (Eds.), *Great Ape Societies*. New York: Cambridge University Press.

Watts, D. P., & Pusey, A. E. (1993). Behavior of juvenile and adolescent great apes. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile Primates: Life History, Development, and Behavior* (pp. 148-171). New York: Oxford University Press.

Wemmer, C., & Fleming, M. J. (1974). Ontogeny of playful contact in a social mongoose, the meerkat, *Suricata suricatta*. *American Zoologist, 14*, 415.

West, M. (1974). Social play in the domestic cat. *American Zoologist, 14*(1), 427-426.

Whiten, A., & Byrne, R. W. (1991). The emergence of metarepresentation in human ontogeny and primate phylogeny. In A. Whiten (Ed.), *Natural Theories of Mind: Evolution, Development and Simulation of Everyday Mindreading* (pp. 267-281). Oxford: Basil Blackwell, Ltd.

Wilkinson, A., Mandl, I., Bugnyar, T., & Huber, L. (2010). Gaze-following in the red-footed tortoise (*Geochelone carbonaria*). *Animal Cognition*, *13*(5), 765-769.

Wilson, S. C., & Kleiman, D. G. (1974). Eliciting play: a comparative study. *American Zoologist, 14*(1), 341-370.

Worch, E. A. (2010). Play behavior of red colobus monkeys in Kibale National Park, Uganda. *Folia Primatologica, 81*, 163-176.

Xitco, M. J., Gory, J. D., & Kuczaj, S. A. (2004). Dolphin pointing is linked to the attentional behavior of a receiver. *Animal Cognition*, 7, 231-238.

Yamagiwa, J., Kahekwa, J., & Basabose, A. K. (2009). Infanticide and social flexibility in the genus *Gorilla*. *Primates, 50*(4), 293-303.

Yokoyama, T., Ishibashi, K., Hongoh, Y., & Kita, S. (2011). Attentional capture by change in direct gaze. *Perception, 40*, 785-797.

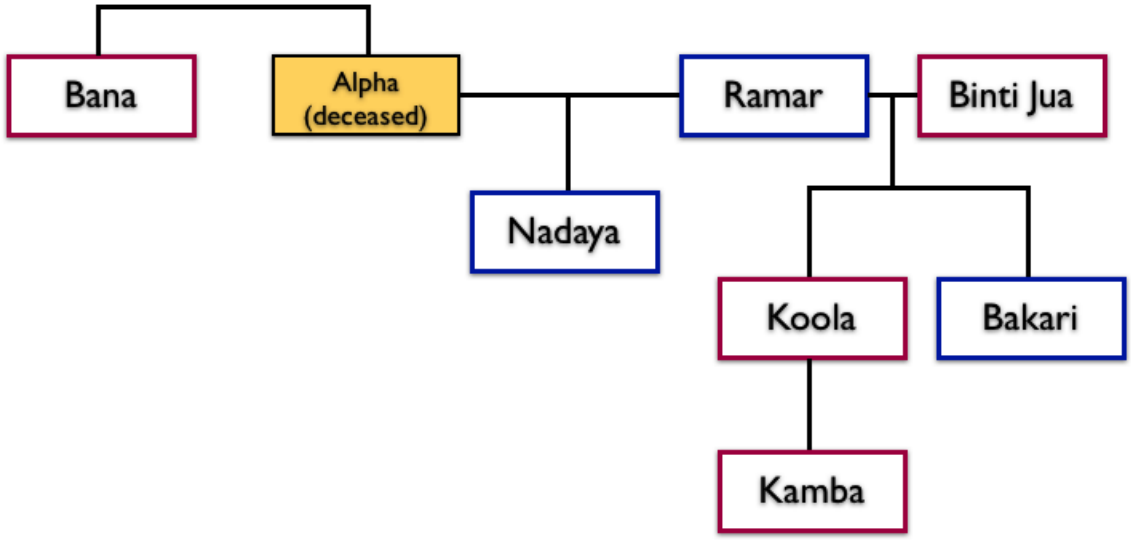
Zahavi, A. (1980). Ritualization and the evolution of movement signals. *Behaviour, 72*(1/2), 77-81.

Zhang, P., & Watanabe, K. (2007). Preliminary study on eye colour in Japanese macaques (*Macaca fuscata*) in their natural habitat. *Primates, 48*, 122-129.

Zimmermann, F., Zemke, F., Call, J., & Gómez, J.-C. (2009). Orangutans (*Pongo pygmaeus*) and bonobos (*Pan paniscus*) point to inform a human about the location of a tool. *Animal Cognition, 12*, 347-358.

Appendices

Appendix A. Brookfield Zoo (Chicago, IL) 2009 gorilla pedigree.



Note: Alpha (48 years old) died at the end of March 2009.

Appendix B. Ethical approval for the Bogart Illusion study (see below).

University of St Andrews
600 YEARS 1413 – 2013

Jessica Mayhew <jm973@st-andrews.ac.uk>

PS5200_Ethical Approval

1 message

psyethics <psyethics@st-andrews.ac.uk> Mon, Mar 2, 2009 at 5:51 AM
To: "Jessica A. Mayhew" <jm973@st-andrews.ac.uk>
Cc: Juan Carlos Gomez <jg5@st-andrews.ac.uk>

27 February 2009

Ethics Reference No: *Please quote this ref on all correspondence*	**PS5200**
Project Title:	**Examining social information sources in primates: The Bogart Illusion and apes**
Researchers Name(s):	**Jessica A. Mayhew**
Supervisor(s):	**Dr. Juan-Carlos Gómez**

Thank you for submitting your application which was considered at the <name> School Ethics Committee meeting. The following documents were reviewed:

1. Ethical Application Form 19.02.2009
2. Participant Information Sheet 19.02.2009
3. Consent Form 19.02.2009
4. Debriefing Form 26.02.2009

The University Teaching and Research Ethics Committee (UTREC) approves this study from an ethical point of view. Please note that where approval is given by a School Ethics Committee that committee is part of UTREC and is delegated to act for UTREC.

Approval is given for completion within the stated time period. Projects, which have not commenced within the time given must be re-submitted to your School Ethics Committee.

You must inform your School Ethics Committee when the research has been completed. If you are unable to complete your research within the validation period, you will be required to write to your School Ethics Committee and to UTREC (where approval was given by UTREC) to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an Ethical Amendment Form submitted where appropriate.

Approval is given on the understanding that the 'Guidelines for Ethical Research Practice' (http://www.st-andrews.ac.uk/media/UTRECguidelines%20Feb%2008.pdf) are adhered to.

Yours sincerely

On behalf of the Convenor of the School Ethics Committee OR Convener of UTREC

University of St Andrews
600 YEARS 1413 – 2013

Jessica Mayhew <jm973@st-andrews.ac.uk>

Mayhew ethical application amendment

psyethics <psyethics@st-andrews.ac.uk> Tue, Nov 23, 2010 at 7:49 AM
To: Jessica Mayhew <jm973@st-andrews.ac.uk>

Dear Jessica

The Convenor of the School Ethics Committee has reviewed your application for amendment and has passed it for approval; the official letter will be issued shortly.

Kind Regards

Helen

--
****
Dr Helen Sunderland
Secretary, School Ethics Committee
School of Psychology
University of St Andrews
St Mary's Quad
St Andrews, KY16 9JP

Tel: +44 (0)1334 462157
Fax: +44 (0)1334 463042

****

[Quoted text hidden]